The Evolution and Development of Inequity Aversion

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ABSTRACT

Humans show such strong sensitivity to whether resources are distributed fairly that they sacrifice personal gain to avoid distributional inequity. This inequity aversion plays an important role in guiding human social decision-making and appears to be ubiquitous across human populations. However, we currently do not understand whether or how inequity aversion evolved over the course of human evolution or how it develops in children.

In this dissertation I examine the evolutionary and developmental origins of inequity aversion using two complementary approaches. First, I ask to what extent inequity aversion is a cognitive trait shared with other cooperative species. Second, I investigate the developmental trajectory of inequity aversion in children by examining (1) the social influences on inequity aversion and (2) the role of reputational concerns in the expression of inequity aversion.

Findings from my dissertation indicate that some nonhuman animal species may react aversively to unequal resource distributions. However, animal reactions to inequity depend on features of experimental paradigms such as whether subjects are required to work for rewards. Furthermore, animals' reactions to inequity do not appear to be an exclusively social phenomenon.

My studies of the development of inequity aversion in children have three important findings: (1) I demonstrate that rejections of inequitable reward allocations are not a signal to experimenters; (2) I provide the first evidence that inequity aversion is not specifically social in children; (3) I show that inequity aversion is sensitive to the presence of an audience.

Taken together, these results make several novel contributions to our emerging understanding of the evolutionary and developmental origins of inequity aversion. First, they indicate that it is important to consider the nonsocial processes that shape aversion to distributional inequity, whether in animals or humans. They also suggest that inequity aversion in humans can be influenced by reputational concerns. Finally, I argue that inequity aversion is an underspecified concept that needs refinement before we can make further progress in understanding how and why it evolved in humans.

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CHAPTER 1

INTRODUCTION

The psychology of distributive justice has been extensively studied using economic games. In these games, human adults routinely sacrifice personal gain in order to achieve equitable outcomes and avoid inequitable outcomes (Dawes et al., 2007; Güth et al., 1982). This 'inequity aversion' is thought to be an important component of human decision-making in the domain of cooperation (Brosnan, 2006, 2011; Fehr & Schmidt, 1999; Raihani & McAuliffe, 2012). Indeed, rejection of inequitable offers in economic games shows considerable cross-cultural consistency (Henrich et al., 2005; Henrich et al., 2006; Paciotti & Hadley, 2003), demonstrating the pervasiveness of inequity aversion in human societies.

Given that inequity aversion plays an important role in human social decision-making, its evolutionary and developmental origins are of considerable interest. Specifically, two questions must be addressed: (1) how did inequity aversion emerge over the course of human evolution and (2) how does it develop in children? My dissertation research used two complementary avenues of investigation to address these questions. The first looks for the roots of inequity aversion in nonhuman species while the second asks how it develops in children aged 4-9 in the Boston area.

This dissertation includes a review (Chapter 2) and four empirical chapters. In Chapter 2 I review evolutionary and developmental perspectives on distributive justice with a particular focus on inequity aversion. I discuss evidence for the expression of

inequity aversion by adults, children and nonhuman animals, and I examine theories for its function in humans and nonhumans. These theories are classified as addressing inequity aversion at either a proximate or ultimate level (Mayr, 1961).

Chapters 3 and 4 address the evolutionary origins of inequity aversion. Recent evidence suggests that the human sensitivity to equality has deep evolutionary roots: several nonhuman animal species show an aversion to unequal reward distributions (Brosnan & de Waal, 2003; Brosnan et al., 2005; Fletcher, 2008; Neiworth et al., 2009; van Wolkenten et al., 2007). Moreover, there is some evidence that nonhuman primates may show sensitivity not just to *equality,* the equal division of resources, but also to *equity*, the relationship between an individual's share of resources and contextual information such as whether they earned their share (Massen et al., 2012; Neiworth et al., 2009; van Wolkenten, et al., 2007). In Chapter 3 I report results from a study that tested this idea by asking whether cotton top tamarins (*Saguinus oedipus*), a cooperatively breeding new world primate, would exhibit a differential response to an unequal reward distribution between themselves and a partner when acquiring rewards was either (1) effortful or (2) effortless. These two conditions were compared to a nonsocial control, where subjects participated in the task without a partner. Seven subjects engaged in a tool-pulling task in which they had an opportunity to pull an unequal distribution of food towards themselves and a partner. Pulling was made effortful by the addition of a weight to the tool. Critically, effort (i.e. the amount of weight) was calibrated to each individual. Overall rates of inequality acceptance were high but subjects were slightly less likely to accept an unequal reward distribution when obtaining it required more effort. Furthermore, individuals varied markedly in their response to effort in this task. While

subjects in my study showed an effect analogous to the human sensitivity to equity, the weakness of the effect and the high inter-individual variation suggest that this capacity is unlikely to be biologically meaningful.

The evolutionary origins of inequity aversion have also been investigated in non-primate taxa (Horowitz, 2012; Raihani et al., 2012; Range et al., 2009; Range et al., 2012). A recent study found that domestic dogs (*Canis familiaris*) are averse to inequitable resource distributions (Range et al., 2009). Range et al.'s report raises the question of whether inequity aversion evolved in social canids as a means of regulating contributions to cooperative activities. Alternatively, inequity aversion in dogs may be a product of domestication by humans. In Chapter 4 I present results from a study designed to distinguish between these alternatives. I tested domestic dogs and a closely related but non-domesticated canid species, the dingo (*Canis dingo*), on the same inequity aversion paradigm. Neither domestic dogs nor dingoes exhibited inequity aversion in this task. These results suggest that the expression of inequity aversion in domestic dogs is dependent on developmental factors and sensitive to the demands of different inequity aversion tasks. Furthermore, these findings indicate that inequity aversion is not a general feature of dingo or domestic dog cognition.

In Chapters 5 and 6 I consider the developmental origins of inequity aversion. Adults and children tend to sacrifice personal gain to avoid both disadvantageous inequity and advantageous inequity (Blake & McAuliffe, 2011; Dawes, et al., 2007; Güth et al., 1982; Loewenstein et al., 1989; Shaw & Olson, 2012). In children these two forms of inequity aversion follow different developmental trajectories, with disadvantageous

inequity aversion emerging early and advantageous inequity aversion emerging later (Blake & McAuliffe, 2011).

Chapter 5 shows my results with children aged 4- to 9- years old recruited from the Boston population. Although inequity aversion is assumed to be a social phenomenon, specific to situations where resources are distributed amongst individuals, the role of social context has not been tested in children. Specifically, it is not clear whether children's rejections of unequal reward allocations are (1) influenced by the social origin of inequitable reward allocations or (2) specific to situations where children are interacting with a social partner. Here I report results from two studies assessing the extent to which these two social factors influence inequity aversion in children. Study 1 ruled out the possibility that children reject unequal reward allocations in order to elicit more favorable offers from the experimenter. Study 2 compared rejections of unequal reward allocations in children interacting with or without a partner (i.e. social vs. nonsocial). Nonsocial factors partly explain rejections of DI when a better alternative is visible. However, social factors play a critical role in eliciting a strong response to inequity. By integrating social and nonsocial factors, these studies provide a detailed picture of the expression of inequity aversion in children and provide insight into its origins in human ontogeny and evolution.

In Chapter 6 I report results from a study that addressed the question: are children truly fair or do they merely want to appear fair when in front of an audience? Reputational concerns are known to be important in influencing human adults' fairness behavior but are little studied in children. In this study I asked whether 6-9-year-old children are more likely to reject advantageously unfair offers of candy (i.e. where the

subject gets more candy than a partner) when in the presence of an audience and a novel peer (their partner) compared to in private. Older children (8-9 years) were more likely to reject advantageous offers than younger children (6-7 years). Across age groups, children rejected advantageous offers when both their partner and an audience were watching. However, when they were in private their rejection tendencies varied by age and gender: older girls rejected advantageously unfair offers regardless of whether anyone could see their decisions. By contrast, older boys tended to accept advantageously unequal offers in private and rejected them in public. Taken together, these results suggest that by the age of 8, reputational concerns have an important influence on the costly enforcement of fairness norms in boys but not girls. These findings challenge the idea that advantageous inequity aversion represents the internalization of a strong norm of fairness and suggest that it may, at least in part, serve as a costly signal.

In Chapter 7, I summarize the main findings from my empirical research. I then situate my findings in the context of the theory laid out in Chapter 2. Finally, I close by suggesting future avenues of research that will further inform our understanding of the evolution and development of inequity aversion.

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CHAPTER 2

THE ORIGINS OF DISTRIBUTIVE JUSTICE: EVOLUTIONARY AND DEVELOPMENTAL PERSPECTIVES

INTRODUCTION

The question of what constitutes a fair or just society has a rich history of debate in philosophy and political theory (Aristotle, n.d./2009; Hume, 1739; Kant, 1785; Plato, n.d./1974; Rawls, 1971). These debates are largely responsible for shaping modern theories of justice, which are influential in today's political and social policy (Sandel, 2010). Modern theories of justice focus on at least three types of justice or fairness[1]: (1) distributive justice, the division of resources among members of society (Rawls, 1971); (2) procedural justice, the process that leads to just outcomes (Rawls, 1971); and (3) retributive justice, how punishment is allocated and administered (Kant, 1785).

In this review, I focus exclusively on principles of distributive justice. The question that is central to the theoretical and empirical work that I review here is: how should resources be divided among members of societies? Scholars in many disciplines, ranging from philosophy to evolutionary biology, have addressed this question. As such, a diversity of methods has been employed to answer questions about the expression and origins of distributive justice. The main focus of my review is on studies that measure individuals' behavior when faced with distributive justice tasks rather than their beliefs

[1] I use the terms 'justice' and 'fairness' interchangeably. While some scholars draw a distinction between fairness and justice (Rawls (1971), for example, considered fairness to be a conception of justice), this distinction is not typically made in the literature reviewed here.

about how resources ought to be distributed. Given this, the bulk of the literature surveyed here is drawn from behavioral economics as well as developmental and comparative psychology. My objective is to situate behavioral results within a conceptual framework that allows us to answer questions of how distributive justice develops in children and whether and how it evolved.

In Part 1, I review theoretical and empirical work that has addressed the question of how and why human adults show a strong sense of fairness and, by extension, why humans show an aversion to unequal resource distributions. In Part 2, I examine distributive justice from a developmental perspective, asking how fairness concerns emerge over the course of human ontogeny. In Part 3, I evaluate empirical support for the idea that some nonhuman species show a concern for distributive justice and, specifically, an aversion to inequity.

PART 1. FAIRNESS IN THEORY AND PRACTICE

1.2. Rational economic models and irrationally generous humans

Normative economic models of decision-making in humans assume that individuals act rationally to maximize personal gain (Camerer, 2003; Camerer & Fehr, 2006). These models predict that, where possible, humans should act selfishly with regards to resource acquisition and distribution. Contrary to this prediction, humans show a striking degree of generosity across different contexts, often donating resources to other individuals even when they are unfamiliar and thus unlikely to reciprocate in the future (Andreoni & Miller, 2002; Bolton et al., 1998; Engel, 2011). Two clear examples of this from

everyday life are the extent to which people (1) donate to charities (Andreoni, 1989; Andreoni & Payne, 2003, 2011) and (2) share resources with others (Gurven, 2004; Hawkes, 1993; Wood, 2006).

Laboratory experiments are able to capture human generosity in a controlled setting (Camerer, 2003). A number of economic games have been developed to investigate the expression and limitations of humans' propensity to share resources (see Box 1. for description of economic games). A striking finding from these games is the degree to which humans contribute, or share, their own resources when they could act selfishly. The clearest example of this is subjects' behavior in the dictator game (see Box 1). In this game, subjects have no incentive to donate resources to another, usually anonymous partner, yet donations are frequent (Engel, 2011). Moreover, generous behavior in the dictator game has been seen not only in industrialized societies (Engel, 2011) but also in non-industrialized societies (Henrich et al., 2005). The finding that these results are not specific to industrialized societies is important due to the fact that behavioral economics studies typically test subjects in western, educated industrialized, rich and developed (i.e. WEIRD) populations, which are probably not representative of most humans (Henrich et al., 2010a, 2010b).

Given humans' willingness to share resources with others, a key question is how do individuals make decisions about when, why and how much to give. In the next section I review evidence that suggests that humans do not share indiscriminately with others. Rather, they tend to be guided by principles of equality and a strong aversion to inequality.

Box 1. Description of common behavioral economics games

Dictator Game
A two-person game in which players typically interact anonymously. Player One is given an endowment of a resource (e.g. money). Player One can offer some or all of his/her endowment to Player Two. There are no penalties for selfishness.

Public Goods Game
An N-person game (i.e. in theory, there is no limit to the number of players) in which players typically interact anonymously. Each player is given an endowment of a resource (e.g. money). In a one-shot game, players are given the opportunity to contribute some or all of their endowment to the public good. Contributions to be public good are then multiplied by a factor and then redistributed equally among all players. The game is thus structured such that highest individual payoffs are achieved if everyone contributes. However, it is in each individual's interest to defect and reap the benefits of others' contributions.

Trust Game
A two-person game in which players typically interact anonymously. Player One is given a relatively small endowment of a resource (e.g. money). Player One can offer his/her endowment to Player Two. If Player One offers the endowment to Player Two (i.e. if Player One 'trusts' Player Two), the endowment is increased by a factor. Player Two can then reciprocate and share the larger endowment or can defect and take the greater endowment for him/herself.

Ultimatum Game
A two-person game in which players typically interact anonymously. Player One is given an endowment of a resource (e.g. money). Player One can offer any portion of his/her endowment to Player Two. Player Two can either accept or reject Player One's offer. If Player Two accepts, they both receive their allocated portions of the original endowment. If Player Two rejects, neither player receives a payoff.

Impunity Game
A version of the ultimatum game (see above) in which Player Two's rejections do not affect Player One's payoff. Thus, Player One may propose any allocation of the original endowment. Player Two may then accept or reject his/her allocated share.

1.3. Adults are averse to unequal outcomes

Human behavior in the dictator game shows that individuals are willing to sacrifice personal gain in order to avoid having more of a resource than another person. These results show that individuals do not measure their reward payoffs in isolation. Rather, individuals gauge their payoffs relative to what others have. Moreover, subjects in the dictator game regularly donate half of their initial allocation (Engel, 2011). These results hint at humans' strong preference for equality under some circumstances (Boehm, 1999; Dawes et al., 2007). Indeed, when humans share resources their allocations tend to be

guided by an *equality* principle; a simple rule dictating that resources should be divided equally among individuals. The clearest demonstrations of the equality principle are found in studies that examine the inverse of equality; namely, inequality.

Loewenstein et al. (1989) asked people to rank their tolerance of different potential resource distributions between themselves and another individual. They found that people considered others' payoffs in addition to their own. Moreover, they found that subjects exhibited intolerance of unequal outcomes. Indeed, subjects exhibited intolerance of unequal outcomes in both directions: when they had less than the other (*disadvantageous* inequality) and when they had more than the other (*advantageous* inequality). It should be noted, however, that intolerance for disadvantageous inequality was stronger than for advantageous inequality.

The concept of inequality aversion has been formalized in theoretical models (Bolton & Ockenfels, 2000; Fehr & Schmidt, 1999). Fehr and Schmidt (1999) defined inequality, or inequity, aversion as willingness to "give up some material payoff to move in the direction of equitable outcomes." In their model, cooperation was facilitated by a small number of individuals that showed aversion to disadvantageous and, to a lesser extent, advantageous inequality.

The evidence that supports the claim of humans tending to sacrifice personal gain to avoid inequality comes from several different economic games (Dawes et al., 2007; Güth et al., 1982; Takagishi et al., 2009). For example, in the impunity game (see Box 1), individuals commonly reject unfair offers, despite the fact that their rejections have no effect on the proposer's payoff (Takagishi et al., 2009). This result shows that, regardless

of the social consequence of rejection, individuals would rather have nothing than accept an inequitable resource allocation.

Individuals also sacrifice personal gain in the face of inequality if doing so affects others' payoffs. Dawes et al. (2007) conducted an experiment where allocations of money were randomly distributed among four players. The players would sacrifice their own money to supplement or decrease others' payoffs in cases of advantageous or disadvantageous inequality, respectively. An important aspect of this result is that individuals were willing to sacrifice their own rewards even when allocations had been randomly distributed, and thus inequalities were not any player's responsibility. This shows that humans were truly reacting to unequal outcomes and not the means by which those outcomes were achieved.

In addition to sacrifice in the face of randomly generated outcomes, individuals also pay to avoid inequality when another player generates inequalities. Results from the ultimatum game nicely illustrate this point (Güth et al., 1982; Murnighan & Saxon, 1998; Rand et al., 2013; Sutter, 2007). In the ultimatum game (see Box 1), individuals regularly reject proposals of less than 20% of the original endowment (Henrich, 2004). Rejections in this game can be construed as punishment or spite (Hamilton, 1970) because individuals incur a cost to deprive another individual of rewards.

Taken together, results from experiments that have explored the extent to which individuals sacrifice personal rewards to prevent inequality suggest that across many types of studies, individuals will readily pay to avoid inequality. However, in the games discussed above, little contextual information is given about the origin of unequal offers. Thus the studies discussed above have demonstrated that humans exhibit a potent

aversion to outcomes but did not address other factors that influence humans' distributive justice decisions.

1.4. Beyond outcomes: distributive justice is sensitive to contextual information

When individuals consider how resources should be distributed and whether to reject inequitable distributions, they consider multiple contextual factors. The four most intensely investigated factors known to affect fairness judgments are the following:

(1) Merit: were resources earned? (1.4.1)

(2) Intentions: was an inequitable allocation intentionally or unintentionally generated? (1.4.2)

(3) Relationships: what is my relationship with the other individual(s) with whom I could share resources? (1.4.3)

(4) Reputation concerns: Are others aware of my decisions? (1.4.4)

I review each of these factors, and their influence on distributive justice, below.

1.4.1. *Merit matters*

When making decisions about what constitutes a fair resource allocation, individuals consider both the outcome and whether recipients deserve a given outcome (Adams, 1963, 1965; Alves & Rossi, 1978; Cook & Hegtvedt, 1983; Konow, 2001; Lamm & Schwinger, 1980; Scott et al., 2001). That is, individuals attend to both equality and *equity*, where equity is defined as sensitivity to merit as well as outcomes (Adams, 1965). For example, most people would think it unfair if a lazy individual were to receive the same payoff as a hard-working individual (a violation of equity). Thus, attention to equity entails an

assessment of the relationship between an individual's reward outcome and their social (or ecological) context.

Despite the recognized importance of equity concerns in guiding individuals decisions about resource distribution, very few studies have examined how equity concerns mediate individuals' *behavior* in economic games. Rather, subjects in these games are given resources instead of having to work for them. Because of this, the effect of equity concerns on adults' distribution decisions remains poorly understood. By contrast, in developmental studies of distributive justice, investigations of equity as distinct from equality are relatively common (Baumard et al., 2012; Kanngiesser & Warneken, 2012; Leventhal et al., 1973). As such, I refer readers to section 2.5.1 where children's' concerns for equity are discussed.

1.4.2 *Intentions matter*

Several theoretical and empirical studies have begun to shed light on the important role that intentionality plays in driving rejections of inequity. These studies show that individuals are more likely to reject intentional unequal offers than unintentional unequal offers (Blount, 1995; Falk et al., 2008; Rabin, 1993; Sanfey et al., 2003).

For example, Sutter (2007) conducted a version of the ultimatum game in which proposers were shown two possible divisions of a sum of money. They were then able to choose one of the divisions to offer to a decider. For instance, in one pair of choices, proposers chose between division that would deliver 50% of a sum of money to the proposer and 50% to the decider and a division that would deliver 80% to the proposer and 20% to the decider. Proposers thus faced a forced choice between two options, and

the decider, who was aware of both options, could accept or reject the proposer's offer. Deciders were likely to reject offers in cases where the proposer could choose between an unequal (80% to the proposer and 20% to the decider) and equal split (50% for both) and decided to choose the inequitable offers. These choices constituted intentional unequal offers. In contrast, deciders were less likely to reject the *same* allocation when the proposer was faced with two identical offers that delivered 80% to the proposer and 20% to the decider (an unintentional unequal offer).

Similarly, Sanfey et al. (2003) found that rejections in the ultimatum game were higher when disadvantageous unequal offers were made by a human partner as opposed to being made randomly by a computer. Notably, however, individuals also rejected many unequal offers made by the computer, even though no human partner would have received the better deal if the offer had been accepted.

Taken together, these results suggest that rejections in the ultimatum game are motivated by more than a strict aversion to unequal outcomes. Rather, individuals mediate decisions based on perceived intentionality of the proposer.

1.4.3. *Relationships matter*

The relationship between individuals importantly influences how tolerant they are of inequity (Clark and Grote, 2003; Fiske, 1992; Loewenstein, 1989). As social closeness between two individuals increases, through relatedness, romantic relationships or friendships, they tend to become less concerned with inequity (Clark and Grote, 2003; Loewenstein, 1989). For example, Fiske (1992) argues that some relationships are characterized by "communal sharing" and individuals in these relationships are unlikely

to track inequities. In contrast, other relationships are characterized by "equality matching" and in these relationships individuals are expected to closely track inequities. There is some recent empirical support for the idea that relationships mediate individuals' concerns for fairness (Clark & Grote, 2003). However, most recent work on distributive justice has used anonymous games, i.e. games where the players are unfamiliar with one another.

1.4.4. *Reputation matters*

Fairness is in numerous cases influenced by reputational concerns. Concerns for both fairness and reputation are illustrated clearly by studies of the dictator game. Individuals are more likely to be generous when their identity will be made known to a recipient compared to when they can play anonymously (reviewed in Andreoni & Bernheim, 2009). Furthermore, individuals in the distributor role in the dictator game will pay a cost to ensure that the recipient is unaware that the game is being played, allowing them to abscond without offering any portion of the original endowment to the other player (Dana et al., 2006). These results show that so-called generous donations in the dictator game are at least partially motivated by reputational concerns as opposed to a motivation for fairness per se.

A second example of the effect of reputation on fairness behavior is seen in a three-player version of the popular ultimatum game. In this modification player one is able to offer a portion of an initial monetary endowment to players two and three. If Player One's offer is accepted then players Two and Three play a second ultimatum game with the offered money. If, on the other hand, player one's offer is rejected, the game is

terminated and no player receives any money. Güth et al. (1996) conducted a version of this game with an important manipulation. In their game, all players knew that the initial endowment could either be large or small, with a known probability. Critically, however, only Player One would know whether the original endowment was large or small in a given round of the game. Under these circumstances Player Ones acted as if they knew that unfair offers would be rejected and thus manipulated the other players' beliefs about the amount of the original endowment. Even in a case of a large original endowment, Player One would offer a fair split of the small endowment amount, suggesting that they hoped to trick Player Twos into thinking that the original endowment had been small. More broadly, this result suggests that fair behavior can be motivated by a desire to meet others' expectations of fairness as opposed to an intrinsic desire for fair outcomes.

Finally, a number of studies suggest that even subtle cues of being watched are sufficient to promote fair behavior in certain situations (Bateson et al., 2006; Burnham, 2003; Burnham & Hare, 2007; Haley & Fessler, 2005; Rigdon et al., 2007).

Together, this body of literature demonstrates that individuals are sensitive to the information that other people can acquire about them in distributional interactions and suggests that they are motivated to appear fair in front of an audience.

1.5. Cultural correlates of inequity aversion

Further evidence that fairness judgments show flexibility within humans comes from studies of distributive justice across different cultures (Henrich, et al., 2005; Henrich et al., 2010; Henrich et al., 2006). These studies show that fairness broadly construed appears to be a universal feature of human psychology, yet fairness concerns are

manifested differently across different populations. For example, Henrich et al. (2005) conducted the ultimatum game in 15 small-scale societies. Results showed that across cultures, individual rejected some of the proposed reward allocations. Thus, nowhere did individuals conform to predominant models of rational economic behavior (which predict the acceptance of any non-zero offer). However, patterns of rejection varied markedly across societies: in some societies stingy offers were rejected, while in others, hyper-generous offers were rejected.

Recent work has also found variation in individuals' behavior on decision-making tasks (Herrmann et al., 2008) and even suggests that individuals may show within- as well as between-population variation in fairness preferences (Lamba & Mace, 2011).

The finding that fairness concerns are ubiquitous (although variable) across cultures raises the possibility that inequity aversion may be an evolved trait in humans and is not social construct. Given this possibility, it is important to consider the factors that may have shaped the evolution of fairness in humans. These ideas are reviewed in the next section and in more depth in Part 3.

Additionally, the finding that fairness concerns vary across cultures indicates that while a sense of fairness may be an evolved trait in humans, there are clearly important developmental factors that shape its expression during the course of human ontogeny. The developmental origins of distributive justice are discussed in Part 3.

1.6. Hypotheses for the evolution of fairness

1.6.1. *Cooperation and the role of punishment*

Cooperation, where one individual provides a benefit to another individual (West et al., 2007), is vulnerable to exploitation by defectors, agents who benefit from cooperative action without investing in cooperation. A number of mechanisms have been proposed as potential stabilizers of cooperation (Axelrod & Hamilton, 1981; Nowak, 2006; Nowak & Sigmund, 2005; Trivers, 1971). One such mechanism is punishment (Boyd et al., 2003; Boyd & Richerson, 1992). By punishing non-cooperativors, individuals can increase the probability of cooperation in the future (Clutton-Brock & Parker, 1995; Raihani et al., 2012).

Theoretical models of the evolution of cooperation show that punishment of defectors can enable cooperation between large numbers of unrelated individuals (Boyd and Richerson 1992; Boyd et al. 2003; Fowler 2005). These models have been supported by results from public goods games where participants have the opportunity to pay to punish individuals that do not contribute to the public good. In these experiments, levels of cooperation are higher when subjects can punish of defectors than when this option is unavailable (Fehr and Gächter 2000a; Dreber et al. 2008). Critically, not only do affected parties punish in these games (i.e., those whose own payoffs have been diminished by defection), but third party observers also punish defectors (Fehr and Fischbacher 2004b).

1.6.2. *The function of inequity aversion*

Sensitivity to inequities in how much individuals have invested in cooperation relative to how much they have benefited, could provide a cue for when to punish poor cooperative partners (Fehr & Schmidt, 1999). Inequity aversion is a possible motivator of punishment in some cases. For instance, rejections of unfair offers in the ultimatum game are a means

of punishing proposers for a low offer. Similarly, punishment in public goods (Fehr & Gächter, 2002) games may be triggered by a reaction to inequity. However, in these cases it is difficult to isolate inequity as the cue that caused individuals to punish. In both ultimatum and public goods games, individuals may punish due to a lower-than-expected payoff (loss aversion; Kahneman & Tversky, 1979, 1984) as opposed to distributional inequality. Moreover, individuals may punish any 'cheating' behavior, regardless of whether it results in unfair payoffs.

To date only one study has isolated inequity aversion as a clear motivation for punishment. Raihani and McAuliffe (2012) conducted a study using Mechanical Turk, an online labor market, in which players made decisions about whether or not to pay to punish in reaction to theft. The study had three conditions. In all conditions, theft occurred (thus controlling for cheating) and players lost the same amount of money (thus controlling for loss aversion). What varied across condition was how loss and cheating affected individuals' payoffs. Sometimes cheating resulted in equal payoffs. Other times it resulted in unequal payoffs. Results showed that individuals most frequently punished cheating when it resulted in a disadvantageous unequal payoff. This finding ruled out loss aversion as the motivation for punishment. Additionally, this study ruled out the possibility that individuals would always punish cheating. Thus, according to these results, disadvantageous inequity aversion can motivate punishment in humans. This lends credence to the idea that inequity aversion functions as a cue to promote cooperation. However, further work is needed to understand whether (1) this is the sole function of inequity aversion and (2) whether inequity aversion motivates punishment in real life.

In addition to its function as an internal cue for punishment, negative reactions to inequity aversion may serve as an external signal to others. By sacrificing personal gain when confronted with inequality, an individual could signal that they are a fair-minded person and thus would make a good cooperative partner (Brosnan, 2011; Takagishi et al., 2009; Yamagishi et al., 2009).

1.6.3. *Social and Nonsocial hypotheses for the evolution of inequity aversion*

I propose that theories to explain the evolution and expression of inequity aversion can be broadly grouped under two hypotheses. First, the *Social Hypothesis* (Brosnan, 2006, 2011; Fehr & Schmidt, 1999) suggests that inequity aversion is specific to the social domain and evolved as a means of regulating contributions to and payoffs from cooperative interactions. For example, if individuals A and B work together to secure a supply of food, but B consumes four times as much food as A then this effort-to-payoff asymmetry may cause A to prevent B from further exploiting the shared resource through punishment. Additionally, A might refuse to cooperate with B in the future. Thus, according to the Social Hypothesis an aversion to inequity allows individuals to ensure that they are not contributing more or less to cooperative activities than fellow cooperators and, ultimately, protects individuals from being exploited and from exploiting others.

Second, the Nonsocial Hypothesis suggests that inequity aversion is a result of domain-general mechanisms such as reference dependence and loss aversion that allow individuals to gauge their own payoffs relative to expected payoffs (Chen & Santos, 2006; Kahneman & Tversky, 1979; Tversky & Kahneman, 1981). According to the

Nonsocial Hypothesis, inequity aversion may be used in social interactions but did not necessarily evolve *for* social interactions. Sensitivity to lower-than-expected payoffs may indeed be useful even in non-cooperative contexts. Attention to how ones' payoffs compare to available payoffs, including those of conspecifics, could confer a benefit in a foraging context where individuals can alter foraging strategies based on information about what payoffs can be expected in a given environment (Chen & Santos, 2006). For example, if individual A has found a small patch of food and sees individual B foraging in a larger patch, A may use information about the unequal resource distribution to inform its decision to abandon its current patch and search for a larger one.

1.7. Summary and open questions

In sum: (1) adults exhibit a surprising degree of generosity in experimental tests of resource allocation; (2) they frequently donate resources to anonymous others even when there are no penalties for selfishness; (3) they exhibit a strong aversion to unequal outcomes but mediate this aversion with attention to the situational factors that lead to unequal outcomes; (4) concerns for fairness appear to be a universal feature of human psychology, but what counts as fair varies by culture; (5) given the ubiquity of fairness concerns, it is possible that fairness represents an evolved trait in humans; (6) the Social Hypothesis proposes that this trait evolved for cooperation, while the Nonsocial Hypothesis proposes that it evolved for nonsocial reasons but may be used in cooperation.

While fairness may play a role in cooperation, evidence reviewed here does not provide strong support for the idea that fairness can stabilize cooperation. In line with the Social Hypothesis, one would expect that groups of fair-minded people would cooperate

more successfully than groups of people with no concern for fairness. While in theory this prediction is met (Fehr & Schmidt, 1999), it has not been tested empirically. Future work on fairness in adults should address this question, as its answer will provide insight into the function of fairness in human societies.

In the next two parts of this review, I examine the developmental and evolutionary origins of fairness.

PART 2. FAIRNESS IN CHILDREN

From a young age children exhibit a strong desire to help others (Svetlova et al., 2010; Warneken et al., 2007; Warneken & Tomasello, 2006, 2007). Children show a willingness to help even when helping is costly (Warneken et al., 2007). Additionally, children as young as 3-year-olds readily work with one-another and with adults on collaborative tasks, suggesting that the ability to form joint intentions with cooperative partners is present from a young age (Hamann et al., 2011; Warneken et al., 2012). Given that cooperative tendencies emerge early during child development, a key question is how children learn to distribute the spoils of collective action.

In this section, I review theories of the development of distributive justice and discuss empirical results indicating that children exhibit a preference for distributional fairness from a young age. I close this section by highlighting gaps in our current understanding of how distributive justice - and inequity aversion specifically - develops during human ontogeny.

2.1. Early theoretical and methodological approaches to child fairness

Traditional theories of the development of distributive justice in children suggest that as children mature they exhibit a stage-like development of fairness concerns (Damon, 1977; Hook & Cook, 1979; Piaget, 1932). In line with this account, children initially exhibit selfish biases in resource distribution tasks and gradually distribute goods according to fairness principles. For example, Damon (1977) suggests that children's reasoning about distributive justice progresses through four stages: Stage 1, children distribute resources according to their own needs and desires; Stage 2, children exhibit a strong preference for equality; Stage 3, children consider external information such as merit and need; Stage 4, children exhibit a developed, nuanced sense of fairness.

Most early work on distributive justice was conducted by presenting children with vignettes and asking them to explain the reasons for their decisions (Damon, 1977). This method provides a powerful tool for gaining direct access to children's explicit notions of justice. However, there are least two potential limitations of this approach. First, children may develop concepts of distributive justice before they are able to articulate such concepts. Second, children may state that resources *ought* to be distributed in one way, while behaving differently when faced with a live distribution task. Given these limitations, there has been a recent methodological shift in studies of distributive justice. Studies increasingly incorporate more direct measures of children's views of how resources should be allocated, frequently borrowing from methods in behavioral economics (Gummerum et al., 2008). In this review, I will principally focus on studies using methods that examine children's behavior in live distribution tasks. For a review of work that primarily used vignettes, see Hook and Cook (1979).

2.2. Infants expect fair distributions

Three recent studies have addressed the question of whether the roots of distributive justice are present in infants (Geraci & Surian, 2011; Schmidt & Sommerville, 2011; Sloane et al., 2012). Each study used variations on a 'looking-time' paradigm (described below) to measure infants' responses to violations of equality.

For example, Geraci and Surian (2011) arranged for 7- to 18-month-olds to watch videos of a *distributor* character allocating two objects between two *recipients*. In the "equal distribution" videos, the distributor allocated the two objects equally between the two recipients. In the "unequal distribution" video, the distributor allocated both objects to one of the two recipients. In both videos, a *third party* character was present as an observer on the screen and watched the allocations. After watching videos of these events, infants watched "test" videos of the third party approaching either the fair distributor or the unfair distributor. To examine infants' reaction to these stimuli, Geraci and Surian focused on two dependent measures. First, they measured how long infants looked at the different test videos. Longer looking times were interpreted as surprise, i.e. a violation of infants' expectation. They found that infants (between 12 months and 16 months) looked longer when the third party approached the unfair distributor than when the third party approached the fair distributor. They interpreted this as indicating that children could distinguish between fair and unfair events and that they expected the third party to interact with the fair character as opposed to the unfair character. Second, they examined infants' choices on a preference test, in which subjects could manually select a picture of either the fair or unfair distributor. In line with the looking-time result, older infants showed a preference for selecting the fair distributor as opposed to the unfair distributor.

The finding that infants expect resources to be distributed equally among agents has been replicated in 15-month-olds (Schmidt & Sommerville, 2011).

Using similar methods, Sloane et al. (2012) asked whether infants not only expect rewards to be distributed evenly (an expectation of *equality*) but also in line with merit (an expectation of *equity*). They tested 19- and 21-month-olds on two experiments. In the first experiment, as in Geraci and Surian (2011), infants expected resources to be distributed equally between two agents. Critically, Sloane et al. showed that this expectation held only when (1) resources were being allocated to live agents (people) and not when they were being allocated to inanimate objects and (2) infants witnessed the distribution of resources and not when the ultimate allocation was unveiled to infants post-distribution. In the second experiment, infants watched two agents complete a task (tidying up toys). In one case, both agents completed the task. In the other case, one agent completed the task while the other played. An experimenter then entered the room and rewarded the agents for completing the task. Findings from this second experiment indicated that infants expected the experimenter to reward agents in proportion to their work effort. Findings from these two experiments indicate that infants have expectations of both equality and equity.

Together, results from these three studies suggest that the roots of a sense of fairness extend into human infancy. These findings are striking in that they suggest that humans have expectations of fairness before they have extensive experience with the social world. Thus, fairness concerns appear to be deeply rooted in human ontogeny. Moreover, these results align with work on early moral development that demonstrates

that preverbal infants are able to make sophisticated moral judgments (Hamlin & Wynn, 2011; Hamlin et al., 2007; Hamlin et al., 2011).

2.3. Children prefer equality

As children age they exhibit a growing preference for equality (Benenson et al., 2007; Blake & Rand, 2009; Damon, 1977; Fehr et al., 2008). Evidence for children's preference for equality comes from studies that have employed a variety of methods, including: sharing tasks (2.3.1), forced choice tasks (2.3.2) and studies that examine children's reactions to violations of equality (2.3.3). A feature that unites the studies reviewed in this section is that children are able to achieve equality at relatively low costs. Subjects either allocate resources among other children or they share some of their own resources, but still keep some for themselves. In the next section (2.4), I discuss cases where children enforce equality by refusing to accept rewards (preferring nothing to inequality) or by destroying rewards.

2.3.1. Sharing tasks

From the age of 25 months, children respond to others' signals of need and show a willingness to share resources (Brownell et al., 2009). As children age, they begin to spontaneously share resources, even in the absence of signals of need.

For example, Benenson, et al. (2007) conducted a dictator game with children aged 4, 6 and 9. In their study, subjects were given 10 stickers and were told that they could donate any number of stickers to another child. Results showed that even the youngest children tended to behave altruistically, donating some of their stickers to the

other child. Older children, on average, donated a greater number of stickers than younger children. These results are broadly consistent with other findings that indicate that children's altruistic behavior increases with age (Harbaugh & Krause, 2000; Murnighan & Saxon, 1998).

Similarly, Blake and Rand (2009) found that children's propensity to donate resources in an anonymous dictator game increased with age in a large sample of 3- to 6-year-olds. In their study, children were given the opportunity to donate preferred stickers and less preferred stickers to an absent, unknown child. They found a dramatic increase with age in the number of children who were willing to donate at least one of their stickers. Subjects who were willing to donate frequently gave half of their stickers to the anonymous other. Their results additionally showed an intriguing effect of value. Children were more inclined to donate their less-preferred stickers than their most preferred stickers, suggesting that resource value influences children's altruistic behavior in the dictator game. Children rarely gave more than half of their stickers, indicating a potential ceiling-effect of equality.

Together, results from the dictator games conducted with children suggest that children's altruistic donations increase with age and that their donations show increasing trends toward equality. In such games, children are able to articulate their opinion that resources should be divided equally (Smith et al., in review). Findings indicate that children aged 3-8 believe both that others should share equally and that they themselves should share equally. However, it is not until the age of 8 that they behave in line with their stated beliefs, and share their own resources equally (Smith et al., in review).

2.3.2. Forced choice tasks

Sharing tasks like the dictator game allow children to share resources spontaneously with others. This is a powerful method for measuring children's spontaneous desires to share. However, sharing tasks make it difficult to isolate the aspects of different resource distributions that children attend to. Forced choice tasks (Fehr et al., 2008; Moore, 2009; Thompson et al., 1997), in which children must decide between two different allocations, offer a way of investigating which aspects of distributional inequity are most important.

For example, Fehr et al. (2008) conducted a forced choice task with 3- to 8-year-olds in which subjects were presented with three different choices. In *prosocial* choices, children decided between an equal allocation of candy (1 for subject, 1 for other; 1,1) and an advantageously unequal allocation of candy (1,0). In this type of choice, a subject could ensure that another child received one candy at no cost to him or herself. In *envy* choices, children decided between an equal allocation (1,1) and a disadvantageously unequal allocation (1,2). In this type of choice, a subject's payoff was static but the recipient's payoff would either be equal or better. Finally, in the *sharing* choices, children decided between an equal allocation (1,1) and an advantageously unequal allocation (2,0). In this type of choice, subjects effectively had to give one candy to another child in order to choose the prosocial option. Results showed a striking age trend in preferences for each choice type. Young children (3-4 years) tended to choose more selfishly across choice trials than older children. Young children were especially selfish in the sharing trials: they rarely chose (1,1) instead of (2,0). Older children, on the other hand, frequently chose the equal option in sharing trials, demonstrating that they were willing to incur a small cost to ensure an equitable resource distribution. In prosocial trials, when

equality could be achieved at no cost, all children of all ages showed a preference the equal option. These findings are broadly consistent with traditional theories of the development of distributive justice. Namely, when sharing entailed a cost, young children exhibited a preference for selfishness while older children exhibited a preference for equality.

2.3.3. Children's reactions to inequality

Another way to investigate whether children show a preference for equality is to test how they react to violations of equality. LoBue et al. (2011) found that 3- to 5-year-old children who had been rewarded unequally for completing a task (tidying up toys) reacted aversively to disadvantageous, but not advantageous, inequity. When children received a relatively bad reward allocation (disadvantageous inequity), they frequently told the experimenter that it was not fair. However, when subjects received a relatively better reward allocation, they expressed that they thought it was fair.

2.4. Children would rather have nothing than accept inequality

The studies reviewed in section 2.3 reveal aspects of the developmental trajectory of inequity aversion in children. However, they do not reveal the extent to which children will sacrifice their own rewards to achieve equitable outcomes. In the studies discussed above, subjects made decisions about different reward allocations but never had to sacrifice their entire payoff in order to achieve equality. In other words, children could achieve equality at relatively low cost. Studies that require children to sacrifice their entire reward allocation, or to discard rewards, provide a clear measure of the strength of

children's preferences for equality and highlight the extent to which children will sacrifice rewards to avoid inequality.

The ultimatum game provides a strong test of children's willingness to sacrifice rewards to avoid inequality. A number of ultimatum games have been conducted with children (Murnighan & Saxon, 1998; Sutter, 2007; Takagishi et al., 2010). In these studies, a proposer offers a reward division to a recipient, who chooses to accept or reject the offer. Young children appear to be more likely to accept low offers than older children (Murnighan & Saxon, 1998). Children frequently make equal offers and these offers are rarely rejected (Takagishi et al., 2010). In contrast, children will sacrifice rewards to reject unfair offers (less than half of the original endowment of resources (Sutter, 2007; Takagishi et al., 2010).

In line with results from the ultimatum game, Shaw and Olson (2012) found that 6- to 8-year-old children disliked distributing rewards unequally in both a third-party task and when making decisions about their own rewards. In their study, children preferred to discard rewards rather than give more or less to one individual. They did this when the overall number of rewards was uneven and thus precluded an equal distribution.

Together results from the ultimatum game with children and from Shaw and Olson (2012) show that children will sacrifice rewards to prevent inequality. However, a limitation of the studies reviewed thus far is that most have been run in artificial situations, where children play one-shot anonymous games. While these design elements have allowed researchers to control for the potentially confounding effects of reciprocity and reputation, they make it difficult to infer how children will behave in real world situations, where repeated interactions are the norm and reputation is commonly stake.

In an effort to address these limitations, Blake and McAuliffe (2011) tested pairs of 4- to 8-year-olds in an all-or-nothing iterated game where unfamiliar children played face-to-face in front of parents and peers. Children were assigned to the roles of actor and recipient. The actor had control over the apparatus and could make decisions about whether to accept or reject reward allocations. The actor's decisions affected both her/his payoff and the recipient's payoff. In this task, the experimenter distributed six equal offers of candy (1 candy for actor, 1 for recipient) and six unequal offers. Unequal offers were either disadvantageous inequity offers (1 candy for actor, 4 for recipient) or advantageous inequity offers (4 candies for actor, 1 for recipient). Actors could accept reward allocations, in which case each child was allowed to take his/her respective allocations. Alternatively, actors could reject reward allocations, in which case neither child received any candy. Results from this study indicated that there was an asymmetry in the development of disadvantageous inequity aversion and advantageous inequity aversion in children. Children as young as 4 were willing to reject disadvantageously unequal offers. However, it was not until 8 years of age that children began to reject advantageously unequal offers. This study is the first to demonstrate that children are willing to give up a relatively large reward to prevent a peer from getting a smaller reward.

Another finding from Blake and McAuliffe (2011) was that children were not automatically reacting to unequal offers. Children across age groups took longer when making decisions about disadvantageously unequal allocations compared to equal allocations. In contrast, only 8-year-old children took longer to make decisions about advantageous unequal allocations.

2.5. Children attend to more than just outcomes

Thus far in this review, I have discussed evidence that suggests that children show a growing preference for equality and a growing aversion to inequality with age. Most of the studies reviewed so far presented subjects with resource allocation tasks in the absence of external information, such as information about merit and intentionality. While such methods allow for the careful investigation of how children react to different types of inequality, they are unable to capture the nuances of children's growing sense of fairness. Indeed, a great deal of evidence suggests that distributive justice in children entails more than attention to unequal outcomes (Damon, 1977; Hook & Cook, 1979). Specifically, there is strong evidence to suggest that children consider the following four factors: (1) whether one individual deserves rewards more than another (merit); (2) whether an unfair offer was intentionally or unintentionally generated; (3) the relationships between the individuals involved in a fairness interaction; and (4) whether others are aware of their actions. While this is not an exhaustive list of the factors that children consider when making distributional decisions, I have selected these four consideration based on the prevalence and quality of available data in the existing literature. I review these four considerations below.

2.5.1. Merit (equity)

In the majority of work discussed thus far, resources were presented to children as windfall gain, meaning children did not have to work for them. While this type of scenario is not uncommon in the life of a child (e.g. parents commonly distribute

resources to children), it is not representative of cooperative interactions where individuals must work together to secure and distribute rewards.

Several studies have investigated the age at which children begin to share the spoils of collective action. From as young as three years of age, children share rewards gained from collaboration roughly equally – even when one individual could keep all the resources for him or herself (Warneken et al., 2011). However, children's willingness to share equally appears to be specific to situations where they work collaboratively to achieve a goal and not when rewards are distributed as windfall gain or when children work separately (Hamann, et al., 2011). These results suggest that children attend not just to the equality of outcomes, but also to aspects of joint effort invested in cooperative activities. Moreover, these results indicate that children's decisions about resource distribution may follow rules of equity in addition to equality.

Leventhal et al. (1973) tested 5-year-olds on an experiment explicitly designed to examine whether children follow equality norms or equity norms. Subjects were told that two absent children had completed a task on the previous day. One of the two children had accomplished more than the other. Subjects were then asked to distribute rewards to the two absent children. Children showed a tendency to give more to the child who had done better than the other, providing there was a large discrepancy in their performance. When one child performed marginally better, subjects reward allocations were not as biased. Even in the former case, however, subjects appeared to be anchored to equality and only distributed a few extra rewards to the better performer (on average, 12 out of 20). Despite the rather small effect, these results indicate that children take merit into account when distributing resources. A more recent study used a similar third-party

distribution task and showed that children as young as three are able to distribute reward by taking merit into account (Baumard et al., 2012).

These studies suggest that children consider merit when making decisions on behalf of other individuals. Kanngiesser and Warneken (2012) recently found that children similarly consider merit when making decisions about their own rewards. In their study, 3- and 5-year-old children worked with a puppet to complete a task. In some cases, the child performed better than the puppet. In other cases, the puppet performed better than the child. Subjects were then asked to distribute rewards between themselves and the puppet. Results showed that children kept fewer rewards for themselves when they had not performed as well as the puppet. However, children rarely gave the puppet more than half of the rewards. Rather, deviations from equality resulted from subjects taking more than half the rewards when they had performed better than the puppet.

Support that distributive justice hinges on perceived merit also comes from a study of adolescents. Using a modified version of the dictator game, Almas et al. (2010) found that subjects were more likely to accept inequality when it arose from differences in relative effort but not when it arose from difference in luck.

2.5.2. Intentions

The finding that adolescents appear to be more tolerant of inequity arising from differential merit but not differential luck suggests that individuals attend to whether inequalities are intentionally or unintentionally generated. Two converging lines of evidence suggest that this is true but that considerations of intentionality do not influence fairness decisions until adolescence. First, children who pass a Theory of Mind task (the

Sally Anne task) make more generous offers in the ultimatum games than those who fail (Takagishi et al., 2010). This finding suggests that the ability to represent another individual's mind leads to more strategic fairness (presumably children make higher offers because they are less likely to be rejected). The ability to represent another individual's mind could be important in allowing individuals to consider whether an opponent intentionally or unintentionally offered an unfair resource distribution. Second, and in line with this idea, 12-year-old children, like adults, are less likely to reject unfair ultimatum game offers when the proposer was unable to make a fair offer (Güroğlu et al., 2009). Younger children, on the other hand, frequently reject unfair offers when the proposer could not make a fair offer (Sutter, 2007) and when unfair offers are randomly generated (Castelli et al., 2010). Thus, the intentional origin of offers appears to play a role in individual's reactions to inequality, but this effect is not seen until relatively late in development.

2.5.4. Relationships

When making decisions about resource distributions, children consider the relationship between potential recipients (Moore, 2009; Olson & Spelke, 2008). They take such relationships into account both when they are involved in the interaction and when they are distributing resources as a third-party.

Moore (2009) found that when 4.5- to 6-year-old children were given the opportunity to share rewards with friends, non-friends, or strangers their allocation decisions varied depending on their relationship with different recipients. When children could donate rewards at no cost, they did so more to friends and strangers than to non-

friends. When donations were costly (i.e. they had to share their own rewards), they donated most frequently to friends. They donated least frequently to non-friends, regardless of costs.

Olson and Spelke (2008) tested 3.5-year-old children's propensity to share with different classes of individuals in a third-party distribution task. In one experiment, they asked children to distribute rewards among dolls and they described the relationships between the dolls: dolls were siblings, friends or strangers. Children biased their distributions away from strangers towards siblings and friends, but did not distinguish between siblings and friends.

Taken together, these results suggest that children consider both their relationship with potential recipients and relationship among recipients when making distributive justice decisions.

2.5.5. Reputation

Results from studies examining children's sensitivity to the presence of an audience indicate that from a relatively young age children understand how others expect them to behave and are importantly influenced by the presence of observers (Aloise-Young, 1993; Banerjee, 2002; Repacholi et al., 2008). Moreover, these results point to reputational concerns that are important in guiding aspects of children's cooperative behavior, such as cheating, sharing and generosity (Bucciol & Piovesan, 2011; Houser et al., 2012; Piazza et al., 2011).

For example, Engelmann and colleagues (2012) showed that the presence of a peer onlooker deterred cheating in 5-year-olds and also encouraged sharing, though the

sharing effect was not statistically significant. In the Engelmann et al. task, children were able to steal or donate a sticker to an absent partner, and subjects were less likely to steal and more likely to donate when being observed by a peer. Similarly, Leimgruber et al. (2012) showed that 5-year-old children were more likely to be generous when they were being watched and when the onlooker was aware of the extent of their generosity.

In a recent study, Shaw et al. (in press) found that 6- to 8-year-old children opted for fair (equal) resource distributions when an experimenter was aware of their actions. However, fewer children opted for fair distributions when they could benefit from inequality without appearing unfair to the experimenter. Thus, distributive justice appears to be influenced by reputational concerns in this age group.

2.6. Summary and open questions

From infancy, children expect resources to be divided equally and equitably among agents. As children age, they show a growing concern for equality, even when achieving equality comes at a personal cost. Children's preference for equality is reflected in their intolerance of inequality. From as young as four years of age, children show a preference for nothing if the alternative to nothing is a disadvantageously unequal reward allocation. However, it is not until later in development that children show a similar reaction to advantageous unequal reward allocations. As children develop, they begin to take external factors into account when making distributional judgments. These factors include merit, intentionality, relationships and audience.

Despite a wealth of available empirical research, there are a number of questions about the development of distributive justice, and inequity aversion specifically, that remain unanswered.

First, the majority of distributive justice experiments that have been conducted to date involve the participation of an adult experimenter. In many studies, experimenters are responsible for distributing reward allocations. Given the involvement of experimenters in these tasks, it is possible that children react to inequality in order to signal their intolerance experimenter as opposed to their partner, whether present or absent. This potential explanation for rejections of inequality has yet to be ruled out.

Second, a latent assumption in studies of distributive justice is that children's reactions to inequity are specific to social contexts, where children are interacting with others or witnessing others interact. While inequity aversion may indeed be a social phenomenon in children, this assumption has yet to be empirically tested.

Third, while it appears that reputational concerns influence how children behave in front of an experimenter, it is not clear whether children try to appear fair in front of peers.

Finally, there is a puzzling tension in results from studies of distributive justice in children. From a young age, children show willingness to spontaneously share their rewards with others. However, it is not until later in development that children react aversively to advantageous inequality. From a conceptual level, these seem like similar situations. In cases where a child shares and where a child is presented with an advantageously unequal offer, the child has relatively more resources than a peer. Why

then do young children show willingness to rectify inequality in the former but not latter case?

3. FAIRNESS IN ANIMALS

Studies of children provide insight into the developmental roots of fairness. However, they tell us little about whether fairness is an evolved trait or one that is inherited exclusively through social and cultural channels. Because children live in an environment with other children and adults, human models may importantly shape their expectations of distributive justice. Investigating the evolutionary roots of fairness in nonhuman animals may provide an opportunity ask which aspects of fairness are present in the absence of human scaffolding.

3.1. Theory: why might inequity aversion have evolved in animals?

The past decade has seen a growing interest in the question of whether the human sense of fairness is unique or shared with other animals. Most work on animals to date has asked whether animals, like humans, are averse to distributional inequity. The main idea motivating work on inequity aversion in nonhuman species is that if inequity aversion helps to regulate cooperation in human societies then it is plausible that inequity aversion serves a similar role in cooperative animal societies. The strongest proponent of this argument is Brosnan (2006; 2011) who suggests that inequity aversion evolved in cooperative human and animal societies as a means of avoiding exploitation in cooperative relationships (Brosnan, 2006; 2011).

The argument that inequity aversion evolved *for* cooperation is central to the Social Hypothesis for the evolution of inequity aversion (discussed in section 1.6.3). The alternative, Nonsocial Hypothesis, states that inequity aversion may be used in cooperation but did not evolve for cooperation. Rather, inequity aversion may be the by-product of a generalized sensitivity to relative distributions of resources (Chen & Santos, 2006; Kahneman & Tversky, 1979; Tversky & Kahneman, 1981).

Studies of animals can help to distinguish between these two hypotheses for the evolution of inequity aversion. This is because the two hypotheses make different predictions about the taxonomic distribution of inequity aversion and the contexts in which inequity aversion should be expressed.

The Social Hypothesis predicts that inequity aversion should be expressed only by cooperative species and only when individuals are interacting with social partners. According to this hypothesis, inequity aversion should not be expressed when lone individuals encounter distributional inequity. Additionally, if inequity aversion evolved as a means of regulating effort-to-payoff ratios in cooperative interactions, individuals should be especially sensitive to violations of equity: cases where relative reward distributions do not map to relative effort.

In contrast, the Nonsocial Hypothesis makes no predictions about the taxonomic distribution of inequity aversion. Rather, this hypothesis predicts that animals will modify their behavior when confronted with a lower-than-expected or lower-than-available distribution of resources. According to this hypothesis, the contexts under which unequal resource distributions emerge are irrelevant. In line with this hypothesis, apparent inequity aversion may be expressed in both social and nonsocial contexts.

3.2. Does animal cooperation require inequity aversion?

Before asking whether inequity aversion is expressed in animals, it is important to evaluate the types of cooperation that exist in animal societies with the goal of understanding whether inequity aversion could, in principle, help to solve the collective action problem in animals. In other words, it is important to evaluate whether inequity aversion could be an ecologically valid solution to the problems that cooperative animals face.

The evolution of cooperation in animal societies can largely be explained by kin selection and mutualism (Boucher et al., 1982; Clements & Stephens, 1995; Clutton-Brock, 2002; Dugatkin, 1997; Hamilton, 1964; Stevens & Gilby, 2004). In addition to these mechanisms, direct and indirect reciprocity may facilitate cooperation in some species (Bshary & Grutter, 2006; Hart & Hart, 1992; Hauser et al., 2003; Krams et al., 2008; Melis et al., 2006; Packer, 1977; Seyfarth & Cheney, 1984; Wilkinson, 1984). Given that most animal cooperation takes place between individuals that benefit either directly (mutualism) or indirectly (kin selection) from investment in cooperative activities, cooperation among animals is probably less vulnerable to exploitation by free riders than cooperation in large groups of unrelated humans. Nevertheless, cooperating individuals still face the challenge of regulating their individual investments in cooperation relative to social partners.

Given this challenge, inequity aversion in the form of an evolved response to unequal work-to-reward ratios could benefit cooperative animals in three ways. First, inequity aversion could prompt individuals to find new cooperative partners (Brosnan,

2011). However, this solution would only work if group sizes were large enough to enable partner switching. Second, inequity aversion could motivate individuals to punish poor cooperators, thereby increasing the probability of future cooperation (Raihani & McAuliffe, 2012a, 2012b). Third, inequity aversion could motivate individuals to up- or down-regulate their investment in collective action.

A critical prerequisite to the utility of inequity aversion in any of these three scenarios is that individuals must vary in their levels of investment in cooperative activities. In the absence of such variation, an aversion to unequal work-to-payoff ratios is unlikely to evolve. In cooperative systems where individual contributions vary, animals could indeed benefit from tracking variation in contributions to cooperation and responding accordingly.

Studies of cooperation in wild animal populations show that individuals in cooperative species show marked variation among individuals in their contributions to cooperative activities (reviewed in Bergmüller et al. (2010)). In some cases this variation can be explained by simple individual differences, such as body size and/or body condition. For example, in wild meerkats (*Suricata suricatta*), individuals that have received supplementary food from an experimenter contribute more to cooperative activities than those who have not been fed (Clutton-Brock et al., 2000; Clutton-Brock et al., 2003). In other cases, however, variation in contributions cannot be explained by condition. For example, studies of bi-parental care in birds show marked variation in how much each parent provisions chicks (Hinde, 2006; Hinde & Kilner, 2007; Johnstone & Hinde, 2006; Jones et al., 2002; Saino & Møller, 1995). Critically, individuals in these species appear to attend to how much the other parent is contributing to offspring

provisioning: when one parent decreases its contribution to care, the other compensates for the drop (Hinde, 2006). This shows that some animals at least have the capacity to attend to relative contributions to cooperative activities and can adjust their own investments in line with others' contributions. In such systems, individuals could benefit from tracking relative contributions to cooperative activities.

These studies demonstrate that individuals in some cooperative animal species vary in their contributions to cooperative activities and have the capacity to respond to an unequal distribution of work by compensating for those who contribute at low levels. However, these studies do not tell us whether individuals are actually *averse* to such inequity. To understand whether animals show an aversion to inequity, experimental tests of animals' responses to unequal reward distributions are needed.

3.3. Experimental tests of inequity aversion in animals

Experimental tests of inequity aversion in captive animals have been conducted on a variety of species. Table 2.1 reviews existing evidence for animal inequity aversion from experimental studies and highlights key design features of the different experimental paradigms that have been used. As is evidenced by the species listed in Table 2.1, the majority of animal inequity aversion studies to date have been conducted on primate species, with a particular focus on capuchin monkeys (*Cebus apella*). Because of this focus, my review of the existing evidence for inequity aversion in animals will be similarly biased towards capuchin monkeys. Additionally, a detailed review of capuchin monkey inequity aversion studies provides a means of (1) illustrating the types of

methodology employed in animal inequity aversion studies and (2) highlighting the key conceptual issues that have emerged from empirical studies of animal inequity aversion.

Brosnan and de Waal (2003) conducted the first experimental test of disadvantageous inequity aversion in a nonhuman primate by asking whether capuchins would refuse to participate in a task where they received a lower payoff than an adjacent individual (partner) for exerting the same effort. In their experiment, two monkeys were placed in adjacent cages and prompted to trade a token for a food reward. In the "equity" condition, both the subject and partner traded tokens for pieces of cucumber, a low value reward. In the "inequity" condition, the partner received a highly valued grape in return for her token while the subject continued to receive a piece of cucumber. Brosnan and de Waal compared these two conditions to two controls: (1) an "effort control", where the partner received a grape without having to trade a token while the subject received a piece of cucumber and (2) a "food control", where a grape was placed in an empty cage adjacent to the subject (the subject could not access the cage) and the subject was prompted to trade for a cucumber. Results showed that capuchin monkeys consistently traded tokens in the equity condition but were less likely to trade in the other conditions. Capuchins were least likely to trade in the effort control, indicating that they were attending to both relative effort as well as relative payoff. Brosnan and de Waal interpreted their findings as the first evidence for inequity aversion in an animal species and suggested that inequity aversion has deep evolutionary roots. However, an additional finding calls into question the strength of this interpretation: subjects also refused to trade in the food control. This result is surprising because it indicates that inequity aversion

may not be specifically social in capuchins and raises the question: why would monkeys refuse to trade when a grape is simple placed out of reach?

Results from Brosnan and de Waal (2003) sparked a controversy about whether capuchins' refusals to trade could be interpreted as evidence for inequity aversion. Four key questions emerged from this controversy. First, why would subjects reject inequity when their rejections have no effect on their partners' payoffs? Second, why would subjects reject a low quality food item in the absence of a social partner? Third, are tasks like the token exchange task important in eliciting an inequity aversion response in subjects? Fourth, to what extent is inequity aversion unique to cooperative animal species? I address each of these questions in turn below.

3.3.1. Why would subjects reject inequity when their rejections have no effect on their partners' payoffs?

When subjects in the Brosnan and de Waal (2003) study refused to trade tokens in the face of inequity, their refusals had no effect on their partner's reward allocation. Partners received a grape regardless of whether or not the subject traded for a cucumber. This design meant that refusals had the effect of increasing inequity between subject and partner as opposed to decreasing it (Henrich, 2004). Rejections in the Brosnan and de Waal (2003) study were thus not analogous to rejections in human inequity aversion tasks like the ultimatum game. In human studies, rejections have the effect of eliminating inequity between two players.

Brosnan and de Waal defended the significance of their results by appealing to results from the impunity game (described in Box 1). In this game, a subject's rejection

has no effect on his/her partner's payoff and thus may represent a signal of general intolerance of inequity (Brosnan, 2011; Takagishi et al., 2009). While this is a plausible explanation for rejections in a task where payoffs are not contingent, a key difference between the Brosnan and de Waal (2003) study and the impunity game in humans is that, in the former, reward allocations are determined by the experimenter whereas in the latter they are determined by the players themselves. This means that if capuchin monkeys' rejections in the Brosnan and de Waal task were indeed a signal of inequity intolerance then they were most likely signaling to the experimenter as opposed to their social partner. Given this, it is difficult to imagine how such rejections could map to inequity aversion during cooperative interactions between capuchin monkeys in wild populations.

Further support for the idea that the task used in Brosnan and de Waal is not analogous to those used in human studies of inequity aversion comes from a study that attempted to replicate the Brosnan and de Waal task with human subjects (Hachiga et al., 2009). In this study, subjects were paid to perform a simple task on a computer. In the test condition, subjects saw that a partner was being paid a relatively higher wage for performing the same task. In contrast to capuchin monkey behavior, this inequity in payment for a job did not result in less work by poorly paid subjects. This finding suggests that humans may be insensitive to inequity in this type of task.

3.3.2. *Why would subjects reject a low quality food item in the absence of a social partner?*

A second critique of the Brosnan and de Waal (2003) study was that capuchin subjects showed high rates of refusal to trade in the 'food control' condition (Wynne, 2004).

Subjects frequently refused to trade with the experimenter when they were unable to access a grape in an adjacent cage. Rejections in this non-social 'food control' suggested that subjects were not necessarily averse to situations where they were disadvantaged relative to a partner. Rather, rejections could have been due to frustration at not being able to access a high value food that was visible to subjects. This idea was further tested in a different group of captive capuchin monkeys (Dubreuil et al., 2006). Indeed, findings from this follow-up study showed subjects were likely to refuse a low quality food item when a better food item was visible but inaccessible.

Another potential source of frustration in the Brosnan and de Waal (2003) task was that subjects reversed roles within the experiment. Role reversals meant that in some cases subjects first exchanged tokens for grapes and later exchanged for cucumber. In these cases, subjects may have formed an expectation that trading a token would result in the delivery of a grape. Thus, it is possible that subjects refused to trade for cucumber because their expectation of receiving a grape had been violated. Indeed the effect of "food expectation" is a well-studied phenomenon in experimental studies of animals (Tinklepaugh, 1928). This idea was tested in a follow-up to the Brosnan and de Waal (2003) study (Roma et al., 2006). In this follow-up study, subjects alternated between receiving a high value food and receiving a low value food. Findings from this study showed that subjects were less likely to accept low quality food if it was offered following high quality food (Roma et al., 2006).

3.3.3. *Are tasks like the token exchange task important in eliciting an inequity aversion response in subjects?*

Together, the follow-up studies described above suggested that subject frustration was an alternative to inequity aversion as an explanation for refusals in the Brosnan and de Waal (2003) task. However, both follow-up studies changed an important feature of the design. In Brosnan and de Waal (2003), subjects were required to work for rewards by trading a token. In contrast, in Roma et al. (2006) and Dubreuil et al. (2006), subjects were simply presented with different food items. If inequity aversion evolved in capuchin monkeys as a means of regulating contributions to and payoff from cooperation, then it is possible that subjects may not have attended to relative reward distributions in the absence of a task that required them to work for rewards (Brosnan & de Waal, 2006).

Indeed, Dindo and de Waal (2007) tested capuchin monkeys on a presentation task where high and low value food items were simply presented to subjects and a partner. They found no evidence that subjects rejected low value food when partners' received a high value reward. They interpreted these findings as support for the idea that the inequity aversion is contingent on the inclusion of a task in experimental tests of inequity aversion.

Further support for the idea that there is an important relationship between effort and inequity aversion came from a replication of the original Brosnan and de Waal study (van Wolkenten et al., 2007). In this version of the study, subjects were tested in "high effort" and "low effort" conditions. In the "high effort" condition, subjects had to trade three tokens for a low value food item while partners were given a high value food item without trading. In the "low effort" condition, subjects had to trade one token for a low value food reward while partners received a high value food item for free. Findings from

this study showed that subjects were least likely to trade in the "high effort" condition, indicating that effort may mediate inequity aversion in capuchin monkeys.

To date, the only studies that have shown support of inequity aversion in capuchin monkeys have included a task (see Table 2.1; Brosnan & de Waal, 2003; Brosnan et al., 2010; Fletcher, 2008; van Wolkenten et al., 2007). However, not all tasks that have included effort have provided evidence for inequity aversion (Brosnan et al., 2006; Fontenot et al., 2007; Silberberg et al., 2006). Thus, at present there is weak support for the idea that the expression of inequity aversion in capuchin monkeys is contingent on the inclusion of a task in experimental tests.

3.3.4. *To what extent is inequity aversion unique to cooperative animal species?*

If inequity aversion evolved as a means of tracking relative contributions to, and payoffs from, cooperative activities then its taxonomic distribution should reflect its role in cooperation (Brosnan, 2011). While the number of animal inequity aversion studies has been growing steadily over the past decade, there are still too few studies to make strong claims about the correlation between cooperation and inequity aversion across species. Nevertheless, positive results from inequity aversion studies have been interpreted as evidence of such a relationship (Brosnan, 2011; see Table 2.1).

Evidence for inequity aversion has been provided from studies of captive chimpanzees (*Pan troglodytes*; Brosnan et al., 2005; Brosnan et al., 2010). However, these studies have suffered from some of the same problems as the early capuchin monkey study (Brauer et al., 2006). Attempts to replicate the effects of inequity in chimpanzees were unsuccessful both in a study that employed a task (Brauer et al., 2009)

and one that did not employ a task (Brauer et al., 2006). Thus, it is unclear whether chimpanzees are inequity averse or whether rejection of inequity could be explained by other reactions such as frustration.

Studies of cotton-top tamarins (*Saguinus oedipus*), a cooperatively breeding New World primate, have shown some evidence of inequity aversion. Both studies completed to date showed that tamarins reacted to disadvantageous inequity (Cronin & Snowdon, 2008; Neiworth et al., 2009). However, reactions to inequity were weak (Cronin & Snowdon, 2008) and dependent on the experimental test employed (Neiworth et al., 2009).

A recent study of long-tailed macaques (*Macaca fascicularis*) found that dominant, but not subordinate, individuals exhibited disadvantageous inequity aversion (Massen et al., 2012). Long-tailed macaques are not known to share food but do show cooperation in other contexts (Massen et al., 2012). Given this, results from this study were interpreted as evidence that inequity aversion may be used in cooperation.

Studies of primates that are not considered to be cooperative include work on orangutans (*Pongo pygmaeus*; Brosnan et al., 2011), squirrel monkeys (*Saimiri spp*.; Talbot et al., 2011). These species were not considered to be cooperative by the study's authors (although see Boinski (1987) for evidence that wild *Saimiri oerstedi* males cooperate to inspect females during the mating season). In experimental tests of inequity aversion, neither orangutan nor squirrel monkey subjects exhibited an aversive reaction to inequity (Brosnan et al., 2011; Talbot et al., 2011).

To further explore the relationship between cooperation and inequity aversion in animals, inequity aversion studies have also been conducted on non-primate species.

Recently, Raihani et al. (2012) asked whether cleaner fish were averse to disadvantageous inequity. Cleaner fish were considered to be an ideal model species for testing inequity aversion because they show extensive cooperation in nature (Bshary & Grutter, 2006) and are known to punish individuals for cheating in cooperative interactions (Raihani et al., 2010; Raihani & McAuliffe, 2012a; Raihani et al., 2012). Raihani et al. (2012) tested inequity aversion in cleaner fish using a task where actor fish had to give tactile stimulation to a plate within a set period of time and then food rewards were delivered to both a partner and the actor. If the actor failed to provide tactile stimulation to the plate, neither the partner nor the actor received their payoff. Despite characteristics that make them suitable for testing, cleaner fish showed no evidence of inequity aversion in this test (Raihani & McAuliffe, 2012a; RaihaniMcAuliffe et al., 2012).

Inequity aversion has also been studied in domestic dogs (*Canis familiaris*). Dogs cooperate both with conspecifics and with humans, making them particularly well suited to experimental tasks that involve a human reward distributor (see Chapter 4). Range and colleagues (2009) conducted the first experimental test of inequity aversion in domestic dogs. Their study resembled the Brosnan and de Waal (2003) experiment, except that instead of trading tokens, subjects were asked to "give paw" to an experimenter in order to receive a reward. They tested pairs of familiar dogs on four test conditions: 1) "equity", where both dogs received a low value piece of food (bread) in return for giving paw; 2) "quality inequity", where the subject dog received bread for giving paw while its partner received a high value item (sausage); 3) "reward inequity", where the subject received no reward for giving paw while its partner received bread; 4) "effort control", where the

subject received bread for giving paw and its partner received bread for doing nothing. These test conditions were then compared to a non-social, "no reward control" condition, where subjects were tested without a partner and asked to give paw for no reward. Range et al. found that dogs refused to give paw more in the reward inequity condition than any of the other conditions, including the non-social control. Thus, dogs in their study showed sensitivity to the absence of a reward but, interestingly, not to differences in reward value (quality inequity condition) or effort exerted in the task (effort control).

Range et al.'s finding that domestic dogs are sensitive to reward inequity is consistent with the idea that because dogs are cooperative, they may have an evolved mechanism for tracking relative payoffs from joint action. However, their results are open to other interpretations for two reasons. First, an alternative explanation is that dogs show sensitivity to inequity due to a history of domestication by humans. At present, this second alternative cannot be ruled out. Second, Range et al. tested only familiar dogs. It is possible that unfamiliar dogs would not be as sensitive to each other's reward distributions. Indeed, Horowitz (2012) tested inequity aversion in unfamiliar dogs, and found no evidence that dogs exhibit an aversion to disadvantageous or advantageous inequity

In sum, based on current data there is weak - if any - evidence for a relationship between cooperation and inequity aversion in animals. In part, this weakness could be due to the fact that criteria for assigning a species to the "cooperative" or "non cooperative" group are not well defined. Additionally, the premise for such assignment is flawed because it assumes that all types of cooperation would be equally vulnerable to exploitation and thus equally improved by inequity aversion. Given the diversity of

cooperation seen in "cooperative" species (Dugatkin, 1997), it is difficult to imagine that this assumption could be met.

Furthermore, it is unclear whether the tasks employed in current experimental investigations of animal inequity aversion adequately capture the social problems that might be solved by inequity aversion in the wild. For example, chimpanzees cooperate across many contexts in the wild (Muller & Mitani, 2005), but do not appear to share food equitably (Gilby, 2006; Stevens, 2004; Stevens & Gilby, 2004). Given this, tasks that ask whether chimpanzees are averse to the inequitable distribution of food may be ecologically and socially irrelevant.

Future work could attempt to refine our understanding of the types of cooperation in wild populations that may benefit from inequity aversion (e.g. food sharing in social canids). Additionally, inequity aversion should be systematically studied in both cooperative and non-cooperative species to better understand whether true links exist between cooperation and inequity aversion in animals. This approach could offer a powerful way of understanding the taxonomic distribution of inequity aversion and its relationship to cooperation.

3.4. Summary and open questions

The goal of this section was to address the question of why inequity aversion might have evolved in animals. The Social and Nonsocial Hypotheses for the evolution of inequity aversion make different predictions about the taxonomic distribution and the contexts (social vs. nonsocial) under which it will be expressed. At present, we have little support

for the Social Hypothesis. Although inequity aversion is expressed in social contexts, it does not appear to be specific to social contexts.

Nonetheless, there is evidence that animals react aversively to the unequal distribution of food. Although these reactions may not be specifically social or specific to cooperative species, they still present an intriguing puzzle: why would an individual sacrifice its own rewards in the presence of inequality?

In order to begin to answer this question, three critical issues must be addressed. First, the relationship between effort and inequality must be better understood. If inequity aversion evolved as a mechanism for regulating work-to-payoff ratios, then individuals should show sensitivity not just to relative reward distributions but also to relative effort. Moreover, it is important to control for inter-individual variation in ability. That is, it is important to show that each individual perceives a given task as effortful.

Second, it is critical to address the roles that humans play in the expression of animal inequity aversion. One way to test this is to investigate whether inequity aversion in domestic dogs is due to a history of domestication by humans or whether it is a result of intra-specific cooperation. If inequity aversion is specific to domesticated dogs (i.e. is not seen in non-domesticated canids) then we would have evidence suggesting that humans helped shape inequity aversion in dogs. This result could have implications in our interpretations of results from other animals with extensive human experience (e.g. captive animals).

Table 2.1. Table summarizing design features and results from inequity studies on animals (table adapted from Jensen (2012)). Column headings are specified as follows: [1]*Cooperative*: is the test species considered to be cooperative? [2]*DI*: did authors claim to provide evidence for disadvantageous inequity (DI) aversion? [3]*AI*: did authors claim to provide evidence for advantageous inequity (AI) aversion? [4]*Task*: were subjects required to participate in a task in order to secure food reward? [5]*Contingent payoffs*: was the test structured such that a subject's refusal affected the partner's reward allocation? [6]*Refusals in nonsocial control*: if a nonsocial control was conducted, did subjects ever show refusal behavior? *Experimenter proposes distribution*: did the reward allocations originate from an experimenter? [8]Sample size (*N*): Total number of subjects that participated in the task. [9]Individual differences reported: did authors report refusal behavior by subject?

Species	Cooperative[1]	DI[2]	AI[3]	Task[4]	Contingent payoffs[5]	Refusals in nonsocial control[6]	Experimenter proposes distribution[7]	*N*[8]	Individual differences reported[9]	Reference
Cebus apella	Yes	Yes	N/A	Yes	No	Yes	Yes	5	No	Brosnan & de Waal, 2003
Cebus apella	Yes	No	N/A	No	No	Yes	Yes	6	No	Dubreuil et al., 2006
Cebus apella	Yes	No	N/A	No	No	N/A	Yes	8	Yes	Roma et al., 2006
Cebus apella	Yes	No	N/A	Yes	Yes	N/A	Yes	10	Yes	Brosnan et al., 2006
Cebus apella	Yes	No	N/A	No	No	N/A	Yes	12	Yes	Dindo & de Waal, 2007
Cebus apella	Yes	No	N/A	Yes	No	Yes	Yes	5	No	Fontenot et al., 2007
Cebus apella	Yes	Yes	N/A	Yes	Yes	N/A	Yes	8	Yes	Fletcher, 2008
Cebus apella	Yes	No	N/A	Yes	No	N/A	Yes	11	Yes	Silberberg et al., 2009
Cebus apella	Yes	Yes	N/A	Yes	No	N/A	Yes	13	No	van Wolkenten et al., 2007
Cebus apella	Yes	Yes	N/A	Yes	Yes	Yes	Yes	10	No	Brosnan et al., 2010
Pan troglodytes	Yes	Yes	N/A	Yes	No	Yes	Yes	20	No	Brosnan et al., 2005
Pan troglodytes	Yes	No	N/A	No	No	Yes	Yes	13	No	Bräuer et al., 2006
Pan troglodytes	Yes	No	N/A	Yes	Yes	N/A	No	11	No	Jensen et al., 2007
Pan troglodytes	Yes	No	N/A	Yes	No	N/A	Yes	6	No	Bräuer et al., 2009
Pan troglodytes	Yes	Yes	Yes	Yes	No	N/A	Yes	16	No	Brosnan et al., 2010
Pan troglodytes	Yes	No	N/A	Yes	Yes	N/A	No	6	No	Proctor et al., 2013
Pan paniscus	Yes	No	N/A	No	No	Yes	Yes	4	No	Bräuer et al., 2006
Pan paniscus	Yes	No	N/A	Yes	No	N/A	Yes	5	No	Bräuer et al., 2009
Gorilla gorilla	No	No	N/A	No	No	Yes	Yes	6	No	Bräuer et al., 2006
Pongo abelii	No	No	N/A	No	No	Yes	Yes	7	No	Bräuer et al., 2006
Pongo abelii	No	No	N/A	Yes	No	N/A	Yes	4	No	Bräuer et al., 2009
Pongo pygmaeus	No	No	N/A	Yes	No	N/A	Yes	5	No	Brosnan et al., 2011
Saguinus oedipus	Yes	Yes	N/A	Yes	Yes	N/A	Yes	8	Yes	Cronin & Snowdin, 2008
Saguinus oedipus	Yes	Yes	N/A	Yes	No	Yes	Yes	5	No	Neiworth et al., 2009 (Study 1)
Saguinus oedipus	Yes	No	N/A	No	No	Yes	Yes	6	No	Neiworth et al., 2009 (Study 2)
Saimiri spp.	No	No	N/A	Yes	No	N/A	Yes	24	No	Talbot et al., 2011
Macaca fascicularis	Yes	Yes	N/A	Yes	No	N/A	Yes	12	No	Massen et al., 2012
Canis familiaris	Yes	Yes	N/A	Yes	No	Yes	Yes	43	No	Range et al., 2009; 2012
Canis familiaris	Yes	No	No	Yes	No	No	Yes	38	No	Horowitz, 2012
Labroides dimidiatus	Yes	No	N/A	Yes	Yes	Yes	Yes	34	No	Raihani et al., 2012

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CHAPTER 3

DOES EFFORT INFLUENCE INEQUITY AVERSION IN COTTON TOP TAMARINS (*SAGUINUS OEDIPUS*)?

INTRODUCTION

Humans show a consistent preference for equal over unequal outcomes (Camerer, 2003; Fehr & Schmidt, 1999; Güth et al., 1982). Individuals sacrifice their own potential monetary gain to avoid both unequal outcomes that put them at disadvantage relative to a social partner (disadvantageous inequity; e.g. Güth et al., 1982) as well as unequal outcomes that put them at an advantage relative to a partner (advantageous inequity; Dawes et al., 2007; Loewenstein et al., 1989). The predominant hypothesis for the function of this 'inequity aversion' is that it allows individuals to regulate relative investment in, and rewards from, cooperative activities (Brosnan, 2006, 2011; Fehr & Schmidt, 1999). By motivating individuals to avoid unfavorable investment-to-rewards ratios, inequity aversion may allow individuals to reduce the extent to which they are exploited in cooperative relationships (Fehr & Fischbacher, 2004a, 2004b; Fehr et al., 2002). Additionally, inequity aversion may help sustain cooperative relationships by motivating individuals to punish non-cooperative partners (Raihani & McAuliffe, 2012a, 2012b).

Previous work has shown that human adults and children show an aversion to two forms of distributional inequity: inequity that results from violations of *equality,* and inequity resulting from violations of *equity (*Adams, 1965; Baumard et al., 2012; Damon,

1977; Hook & Cook, 1979; Kanngiesser & Warneken, 2012; Sloane et al., 2012). A concern for equality means that individuals tend to prefer equal outcomes to unequal outcomes. A large body of work in humans has found that in the absence of contextual information, individuals strive for equality (Benenson et al., 2007; Camerer, 2003; Dawes, et al., 2007; Fehr et al., 2008; Henrich et al., 2005). A concern for equity, on the other hand, is more nuanced. Individuals temper their preference for equality with information about features of the social environment in which inequity occurs (Adams, 1965; Hook and Cook, 1979). Such information may include evidence of differential work effort or need. For example, most people would think it unfair if a lazy individual were to receive the same payoff as a hard-working individual (a violation of equity). In the absence of information about workload, however, most people would expect both individuals to be rewarded equally (a violation of equality). Thus, a key distinction between the equality and equity is that the latter entails an assessment of the relationship between an individual's social or ecological context as well as their reward outcomes while the former is focused solely on reward outcomes.

While a distinction between equity and equality is not always made in experimental studies of inequity aversion (e.g. Blake and McAuliffe, 2011; Brosnan and de Waal, 2003), here we highlight this distinction because we are particularly interested in violations of equity. Specifically, we are interested in cases where individuals show sensitivity to invested effort relative to reward distributions (i.e. equity) rather than to reward distributions alone (i.e. equality). These cases are critical to understanding the relationship between inequity aversion and cooperation. If individuals show an aversion only to violations of equality and not to violations of equity then it is unlikely that

inequity aversion serves an important regulatory function in cooperative relationships. We follow the convention of using the term inequity aversion to mean an aversion to violations of equity and/or equality but, where necessary, we are careful to specify whether equality or equity is our focus.

Inequity aversion in nonhuman species

The extent to which humans' sensitivity to inequity is shared with other species was first studied by in captive brown capuchins (*Cebus apella;* Brosnan & de Waal, 2003). In this study, the authors asked whether capuchin monkey subjects would refuse to participate in a task where they received a lower payoff than an adjacent individual (partner) for exerting the same effort. In their task, two monkeys were placed in adjacent cages and prompted to trade a token for a food reward. In the equal condition, both subject and partner traded tokens for pieces of cucumber, a low value reward. In the unequal condition, the partner received a highly valued grape in return for her token while the subject continued to receive a piece of cucumber. Brosnan and de Waal compared these two conditions to two controls: (1) an "effort control", where the partner received a grape without having to trade a token while the subject received a piece of cucumber if they traded and (2) a "food control", where a grape was placed in an empty cage adjacent to the subject and the subject was prompted to trade for a cucumber. Results showed that capuchin monkeys consistently traded tokens in the equity condition but were less likely to trade in the other conditions. Capuchin monkeys were least likely to trade in the effort control, indicating that they were attending to relative effort ("equity") as well as to equality of relative payoffs. Findings from this study suggested that capuchins were not

only sensitive to the distribution of rewards but also were reluctant to participate in the task when rewards were distributed inequitably with regards to labor. Brosnan and de Waal's (2003) study was the first to demonstrate that a nonhuman species showed an aversion to inequity. The authors argued that their results provided evidence that inequity aversion has deep evolutionary roots. Furthermore, because their findings highlighted the potential role of effort in mediating an aversion to unequal outcomes, the authors suggested that their results were consistent with the idea that inequity aversion evolved as a means of regulating ones investment in, versus gains from, collective action (Brosnan and de Waal, 2003; Brosnan, 2006).

Brosnan and de Waal (2003)'s study has since been critiqued both for aspects of its design (Henrich, 2004) and its interpretation (Henrich, 2004; Wynne, 2004). For example, their claim that monkeys showed human-like inequity aversion may be unsubstantiated because their study did not use a contingent payoff structure common to human inequity tasks (Güth et al., 1982). When subjects rejected low value food items in their task, their rejections did not affect their partner's reward (Henrich, 2004). Rejections thus increased inequity between the two monkeys rather than decreasing it.

In addition to this paradoxical result, the Brosnan and de Waal (2003) findings are contentious because attempts to replicate the effect of inequity aversion in capuchin monkeys have yielded mixed results (Roma et al., 2006; Silberberg et al., 2006; van Wolkenten et al., 2007). One study successfully replicated the effect of inequity aversion in capuchins (van Wolkenten et al., 2007). However, others have attempted to replicate and have not found evidence for inequity aversion (Roma et al., 2006; Silberberg et al., 2006).

The claim that a human-like sense of inequity aversion has deep evolutionary roots has further been challenged by the fact that inequity aversion studies conducted on other animal species have generated a similar range of equivocal findings (e.g. chimpanzees (*Pan troglodytes*): Brosnan et al., 2005; Brauer et al., 2006, 2009; Jensen et al., 2007) and domestic dogs (*Canis familiaris*): Horowitz, 2012; Range et al., 2009; Range et al., 2012. For example, Brosnan et al. (2005) found that chimpanzees, like capuchin monkeys, show sensitivity to inequality in a token exchange task. Subjects in their experiment showed reluctance to exchange tokens for a low quality food item if they had just observed a social partner receive a more desirable food item. In contrast, Brauer et al. (2006) found no evidence for inequity aversion in chimpanzees and suggested that apparent inequity aversion might be better explained by frustration at not being able to obtain a desirable food reward.

It is not yet clear why some animal studies generate evidence for inequity aversion while others do not. One possible explanation for inconsistencies between different studies relates to the experimental paradigms used. The studies that have generated evidence for inequity aversion in animals have required subjects to perform a task in order to secure a reward (Brosnan & de Waal, 2003; Brosnan et al., 2005; Neiworth et al., 2009; Proctor et al., 2013; Range et al., 2009; Range et al., 2012). In other words, they have arranged for subjects to work for rewards. In contrast, two of the studies that have not found support for inequity aversion did not require subjects to perform a task in order to secure rewards (Brauer et al., 2006; Roma et al., 2006, discussed in Brosnan, 2011). Instead, subjects in these studies were simply presented with unequal reward allocations.

The effort hypothesis

This pattern in inequity aversion findings has lent support to the hypothesis that inequity aversion is linked to work effort (hereafter, the "effort hypothesis"). The logic behind this hypothesis is as follows: if the function of inequity aversion is to maximize the benefit from a cooperative relationship, selection is expected to favor a response that is sensitive to the partner's work effort (Brosnan, 2006, 2011). An important caveat to the effort hypothesis is that while effort may be necessary to elicit an inequity aversion response in animals, it is certainly not sufficient. Indeed, several studies have used paradigms that required subjects to work for rewards and yet have failed to show evidence for inequity aversion (Brauer et al., 2009; Brosnan et al., 2011; Horowitz, 2012; Jensen, et al., 2007; Raihani & McAuliffe, 2012a; Raihani et al., 2012; Silberberg et al., 2009; Talbot et al., 2011). Nevertheless, the effort hypothesis remains a compelling explanation for the distribution of evidence for inequity aversion across different animal studies.

A number of studies have indirectly addressed the potential influence of effort on inequity aversion in animals (Brosnan and de Waal, 2003; Dindo and de Waal, 2007; Neiworth et al., 2009; Range, 2009, van Wolkenten et al., 2007). For example, Dindo and de Waal (2007) presented pairs of capuchin monkeys with unequally valued food items in the absence of a task. Subjects in their study did not exhibit an inequity aversion response. This result was consistent with the idea that inequity aversion is specific to situations where subjects are tracking work effort relative to rewards and is not evinced in situations of unequal rewards in the absence of work. Similarly, Neiworth et al. (2009) directly compared a token exchange task with an offering task in a single group of cotton-top

tamarins (*Saguinus oedipus*). In their exchange task, like the task in Brosnan and de Waal (2003), subjects traded a token in exchange for a reward while their social partner received a more attractive reward without trading. In the presentation task subjects were simply offered an unequal division of resources. This study found that subjects only showed an inequity aversion response in the exchange task and not in the offering task.

Finally, van Wolkenten et al. (2007) manipulated effort in a study of inequity aversion on capuchin monkeys. Subjects were tested in a paradigm that was almost identical to that administered in Brosnan and de Waal (2003). In this study, however, subjects were tested in an additional "large effort" condition where they were required to trade three tokens for a food item while their partner received the same reward or a better reward for free. They found that the large effort condition magnified subjects' aversive response to inequity. Subjects were least likely to participate in the task when they had to trade three tokens to secure a low value food item while their partner was given a high valued food item for free.

While these studies show that the inclusion of a task that requires subjects to exert effort for their rewards appears to affect subjects' responses to inequity, it is unclear whether subjects tested in these studies perceive such tasks as effortful. Previous studies have made two critical, yet untested, assumptions. First, previous work has assumed that (1) tasks like the token exchange task are perceived as effortful by subjects and (2) that for any given task, the degree of effort is perceived homogenously across individuals. Some data suggest, however, that subjects may readily engage in token exchange tasks for any reward, regardless of its size. For example, Lakshmininaryanan et al. (2008) found that capuchin monkeys were willing to exchange a token for a single oat. In their

group of capuchins, a single oat is considered to be the lowest valued food item (Laurie Santos, *personal communication*), yet capuchins were still willing to exert effort to obtain it in a token trading task. The finding that subjects were willing to trade a token for such a low value item suggests that they did not perceive the exchange itself to be prohibitively effortful.

Given that past work has not tested the assumption that subjects perceive token exchange tasks and similar tasks to be effortful, we currently lack a firm understanding of the influence of effort on inequity aversion in animals. An alternative explanation for past results demonstrating that the inclusion of a task is important in inequity aversion experiments is that such tasks may make the experiments more salient to subjects. This increased salience could in turn make subjects more attentive to unequal reward distributions. If this were the case, we would have evidence that animals attend to and are averse to violations of equality but no evidence that they are averse to violations of equity. Due to the limitations of previous work addressing the effect of effort, this alternative explanation cannot be ruled out.

Current study

In the present study we provide a strong test of the effort hypothesis by asking whether effort mediates inequity aversion in cotton-top tamarins. Our experiment includes two key design features. First, we directly calibrated work effort to each subject's individual ability. In our task, subjects were given an opportunity to accept or reject reward allocations that provided a more desirable reward to a recipient than to the subject. Subjects could accept or reject reward allocations by pulling or not pulling a tool,

respectively. We directly manipulated effort by making the tool as heavy as possible from the perspective of each subject. We did this by determining the maximum amount of weight each subject would consistently pull to receive a single piece of food under solo conditions. With this method, we demonstrated that the task was effortful to all subjects. Having established that the task was effortful, we were able to test the conditions under which individuals would or would not work for an unequal division of rewards. Critically, the inclusion of the pulling task itself was kept constant across conditions.

Second, subjects' rejections (i.e. inhibited pulls) in our task affected not only the subjects' payoff but also their partners' payoff. In other words, our task had a contingent payoff structure. When a subject refused to pull not only were they prevented from accessing their rewards but their refusal also prevented recipients from accessing rewards. This design feature is equivalent to human tests of the inequity aversion where subjects make decisions for both themselves and a partner (e.g. Blake and McAuliffe, 2011; Güth et al., 1982). This design feature was in response to a previous critique of past work on animal inequity aversion that suggested that rejections in a non-contingent task were increasing rather than decreasing inequity between players (Henrich, 2004).

Cotton top tamarins were a well-suited model species for this study for four reasons. First, cotton-top tamarins are cooperative breeders. Mothers and fathers rear offspring in monogamous pairs with help from older offspring that have not yet dispersed and, occasionally, from immigrant adults (Snowdon, 1996). Because they cooperate extensively with conspecifics, cotton-top tamarins may need to regulate their investment in cooperation in relation to how much others are investing. Thus, this species may show particular sensitivity to the relationship between work effort and rewards. For example,

cotton-top tamarin helpers assist breeding individuals with infant care. One way in which they assist is by carrying infants. Infant carrying is a costly behavior as it decreases individuals' foraging time (Price, 1992) and is energetically expensive (Achenbach & Snowdon, 2002; Sánchez et al., 1999). Helpers' contributions to infant care are thought to be beneficial because infant survival increases with increasing group size (Savage et al., 1996). Higher infant survival may ultimately benefit helpers because cotton-top tamarins gain direct benefits through increased group size (e.g. through increased predator detection; Savage et al., 1996). Thus, cotton top tamarins benefit from cooperation but cooperation is costly and thus vulnerable to exploitation by individuals who contribute relatively little to collective action. Second, it has been hypothesized that cooperative breeders show increased social tolerance and social attention compared to non-cooperative breeders and may thus be more sensitive to their social partner's rewards (Burkart et al., 2009; Burkart & van Schaik, 2010). Given this, one would expect tamarins to be more likely to exhibit inequity aversion than less socially tolerants species. Third, an experimental test of prosocial behavior in another cooperative breeder, the common marmoset (*Callithrix jacchus*), demonstrated that marmosets show prosocial motivations in a task where subjects could spontaneously offer food to a partner (Burkart et al., 2007). The authors suggested that other cooperatively breeding primates would also show attention to conspecifics' rewards (although see Cronin et al., 2009 and Stevens, 2010), although this has not yet been extensively tested. Finally, cotton-top tamarins have previously been tested in inequity aversion paradigms before and have shown evidence of a response to unequal reward distributions (Cronin et al., 2008; Neiworth et al., 2009).

To test whether effort influenced inequity aversion in cotton-top tamarins, we designed three experimental conditions. Across conditions, inequity was held constant: the subject was always given one item and their partner always received four items. This distribution was used because we were confident that tamarins could reliably distinguish these quantities (Stevens et al., 2007). We then used three different conditions to manipulate two different aspects of the context under which inequity was presented: 1) the effort required to accept unequal offers and 2) the presence of a social partner. First, in the *Inequity* condition, subjects had to complete a task (pull the tool) in order to be rewarded but the task required minimal effort. Subjects' rate of pulling in the Inequity condition provided us with their baseline response to inequity in this task. Second, in the *Weighted Inequity* condition, subjects had to exert effort to access an unequal allocation of rewards. In this condition, subjects were faced with a large inequity in effort in addition to an unequal resource distribution: the subject had to perform an effortful task that resulted in their partner receiving a more attractive reward for no effort. Third, in the *Weighted Nonsocial Control* condition, the subject had to exert effort to access an unequal allocation of reward but did so in the absence of a social partner. That is, the more attractive reward was presented to an adjacent empty cage rather than a cage occupied by a recipient partner. By comparing this condition to the Weighted Inequity condition, we could test whether tamarins' responses to inequities of effort were specific to a social context.

The main measure of interest in this study was subjects' rate of pulling. We reasoned that if subjects were averse to inequities of effort then they would be least likely to pull in the weighted conditions compared to the non-weighted condition. Furthermore,

if subject's aversion to inequities of effort were specifically social then subjects would only be reluctant to pull the tool in the Weighted Inequity condition and they would be motivated to participate in the Weighted Nonsocial Control condition. However, subjects may have reacted to the experimental conditions in ways not evident in their raw pulling behavior. For example, subjects may have shown initial reluctance to pull in some cases but eventually pulled, and this hesitation would not be apparent in raw pulling scores. To gain insight into their decision-making processes we therefore measured subjects' reaction time on each trial to test whether they were faster to make decisions in some conditions than others (Blake & McAuliffe, 2011; Piovesan & Wengstrom, 2009; Rand et al., 2012).

METHODS

Subjects

Subjects were adult cotton-top tamarins from a captive colony housed in the Cognitive Evolution Laboratory at Harvard University. Seven subjects (four females, three males; see Appendix 1, Table A1.1 for subject information) participated in the study as *actors*. Twelve subjects participated as *recipients*. Recipients included the seven actors and five additional individuals (two females, three males).

All subjects were born in captivity and lived in mated pairs with young offspring (where applicable) in separate home cages. Subjects were fed a daily diet of monkey chow, fruit, seeds and mealworms and had ad libitum access to water in their home cages. All subjects had previously participated in a number of cognitive tasks, including a

previous study on inequity aversion. Four subjects (SH, RB, EM and PB) had additionally participated in a study on other-regarding preferences (Stevens, 2010).

Subjects were paired with recipients of the opposite sex. Pairings were designed in this way because pilot testing indicated that same-sex pairs were not relaxed when placed together in the testing apparatus (see Appendix 1, Table A1.1 for pairings). Subjects were never tested in a pair with their mate since responses to inequity might be influenced by interdependencies in fitness (Raihani, et al., 2012; Roberts, 2005). Where there was a role-reversal within an actor-recipient pair, sessions were separated by at least two weeks in order to reduce the possibility of direct reciprocity within pairs.

Apparatus

Subjects were tested in an apparatus consisting of two adjacent cages (Fig. 3.1; see Appendix 1, Fig. A1.1 for measurements). Each cage had a small door that was connected to a solenoid valve with nylon thread. The experimenter opened and closed doors using remote switches that were connected to the solenoid valves. Actors were always placed in the cage on the left side of the apparatus. From this cage, actors could access a tool when the apparatus doors were open. The tool was connected to a sliding tray. Two food dishes were affixed to the sliding tray. One of the food dishes was aligned with the actor's door, the other with the recipient's. When an actor pulled the tool, the sliding tray moved closer to the cages, giving both the actor and the recipient access to the food dishes.

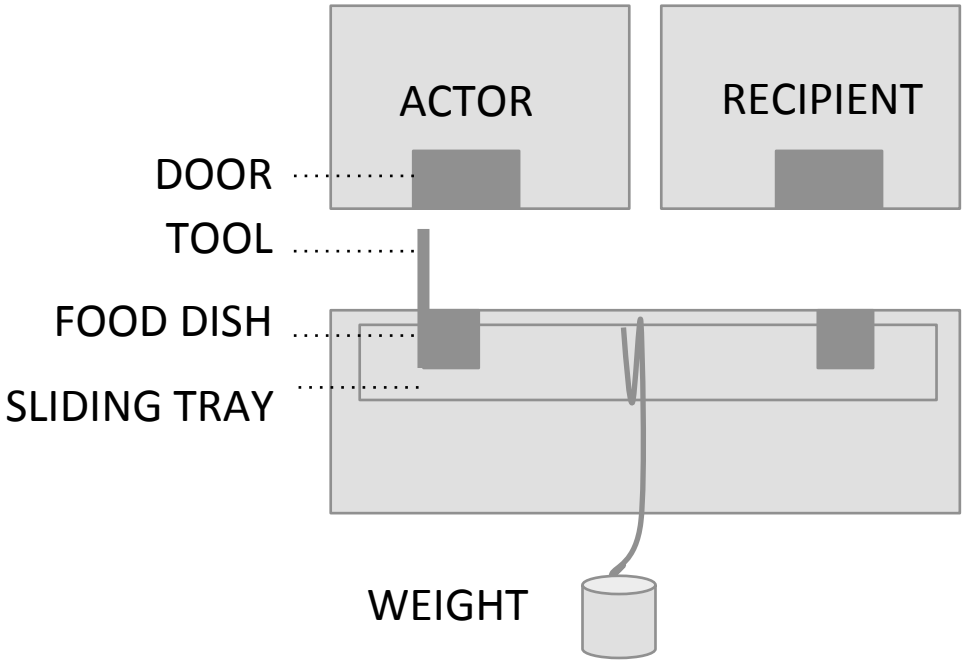

Figure 3.1. Diagram of the testing apparatus. Actor and recipient were placed in adjacent cages, with the actor always placed in the cage on the left. Each cage had a door that was attached to a solenoid valve that could be remotely controlled by the experimenter. When the doors were open, the actor could pull the tool, thereby bringing the sliding tray supporting two food dishes towards the cages allowing subjects to reach their food rewards. In weighted conditions, a small container holding metal disks was attached to sliding tray with a rope and hung off the apparatus, thereby making the tool pulls effortful. In the non-weighted condition, the container remained attached to the sliding tray but rested on the table, thus adding no weight to the pulls.

In the weighted experimental conditions, a plastic container of metal disks (the weight) was attached to the sliding tray using thick cord. The weights container was then hung off the side of the table upon which the apparatus sat. This set-up meant that the sliding tray was held back by a hanging counterweight. When pulling the tool, subjects had to overcome the weight of the counterweight in order to bring the sliding tray toward the apparatus doors. To provide subjects with a visual cue that a weight was attached to the apparatus, a bright yellow piece of foamcore was attached to the tool during weighted sessions. During the non-weighted condition this piece of foamcore was absent.

Additionally, during non-weighted sessions the plastic container remained attached to the sliding tray but rested on the table and therefore did not add weight to tool.

When participating in the pulling task, subjects would typically pull the tool toward the apparatus doors and then let go of the tool in order to eat the food items contained in the dishes. In the weighted conditions, letting go of the tool would result in the sliding tray being quickly pulled away from the apparatus by the counterweight. In order to prevent this, and thus allow the subject to access the food rewards, the experimenter would surreptitiously eliminate the weight by holding it in place once the subject had moved the tray passed a line marked on the apparatus base with silver tape (approximately 10 cm from the door).

Food rewards used in this study were small pieces of Froot Loops® breakfast cereal and small pieces of raisin. All actors but one (LS) were tested with Froot Loops. LS and her recipients were tested with raisins because she refused to eat Froot Loops.

Conditions and research design

Subjects were tested in three conditions in each actor-recipient pair. In all conditions, food rewards were distributed unequally: the actor received one food item while the recipient received four items. While reward distribution was held constant, both social context and effort were varied across the three experimental conditions (Table 3.1).

Table 3.1. Names and descriptions of conditions

Condition name	Description	Recipient?	Effort
Inequity (INEQ)	Actor receives 1 piece of food, while recipient receives four pieces. No weight is attached to the tool.	Yes	No
Weighted Inequity (INEQ-W)	Actor receives 1 piece of food, while recipient receives four pieces. Weight is attached to the tool.	Yes	Yes
Weighted Non-social Control (NSC-W)	Recipient absent. Actor receives 1 piece of food, while four pieces of food are placed on recipient's tray. Weight is attached to the tool.	No	Yes

First, in the Inequity (INEQ) condition, the actor was paired with a recipient and the tool was not weighted. This condition was designed to assess actors' baseline levels of rejection of inequity in a social context. Second, in the Weighted Inequity condition (INEQ-W), the actor was paired with a recipient and the tool was weighted. This condition was designed to test whether actors would be willing accept a disadvantageous reward allocation if doing so was effortful. Third, in the Weighted Non-social Control (NSC-W), no recipient was present and the tool was weighted. This condition was designed to control for the fact that a potential decrease in pulling in INEQ-W compared to INEQ might be a response to the effortful acceptance of inequity regardless of social context. If so, subjects would be expected to pull less in both weighted conditions compared to INEQ. If, on the other hand, subjects are averse to the effortful delivery of a relatively better reward to a partner, then reduction in pulling should be specific to the INEQ-W condition.

Subjects were tested with recipients in blocks of three sessions ("recipient blocks"): one session for each of the three conditions. Sessions were run on separate days. The order in which conditions were run was counterbalanced within subject and between recipient blocks as well as between subjects. Each session consisted of 12 trials. Recipient blocks were separated by a *mixed solo session* (see below).

Weights training

All actors tested in this study had previously been trained to pull a tool for food rewards for a previous inequity aversion study (McAuliffe, unpublished data). The focus of weights training was two fold: (1) we aimed to train subjects to pull a weighted tool and (2) we aimed to establish how much weight each actor was willing to pull for one food reward.

In order to train subjects to pull a weighted tool, subjects were first tested in *weighted solo* sessions. In these sessions, actors were placed in the apparatus in the absence of a partner. Like test sessions, solo sessions consisted of 12 trials. On each trial, an experimenter placed one food item in the actor's tray, opened the door and allowed the actor to pull the tool. In initial training sessions, a weight was added to the tool and the amount of weight was gradually increased to get a sense of how much weight an actor would consistently pull for a single reward. Once an actor was able to pull the weighted tool in order to access one food item for 12/12 trials on two consecutive sessions, we increased his or her weight by one metal disk. This increase in weight amounted to an increase of approximately 22g, although individual metal disks varied slightly in weight. This process was iterated until the addition of one unit of weight reduced the subject's

pulling by at least 20% (10/12 or less). Once this decrease in pulling occurred, we returned to the subject's previous weight. This previous weight was then considered to be the maximum weight a particular subject was willing to pull to acquire 1 food item.

This method allowed us to calibrate weights to individual subjects. Thus, we ensured that "effort" in this task was defined by each individual's propensity to pull a weighted tool. Fig. 3.2 shows the striking variation in the weight that subjects were willing to pull as measured as a proportion of each subject's body weight. Final weights for each subject were as follows: RB, 155g; SH, 268g; EM, 68g; LS, 381g; PJ, 92g; SD, 203g, RA, 292g.

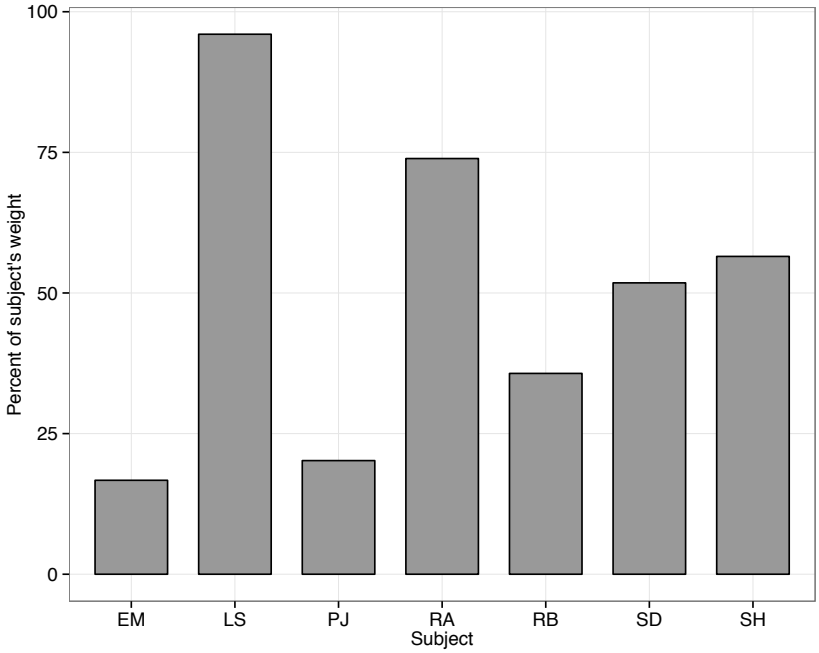

Figure 3.2. Bar plot showing individual differences in the maximum weight that subject were willing to pull for one food item. Weights are displayed as a percentage of subjects' body weight. Individuals were trained to pull a weighted tool and weights were gradually increased until a 1unit increase in weight (an increase of approximately 22g weighted disk) caused pulling to drop by at least 20%.

Pre-test sessions

Following the weighted solo sessions, we ran non-weighted and weighted *mixed solo* sessions. Actors were first tested in mixed solo sessions where the tool was not weighted. Mixed solo sessions were designed to ensure that subjects were attending to the distribution of rewards between the actor and recipient trays. These sessions consisted of 12 trials. These 12 trials were comprised of four trials of each of three trial types: 1) 1-1 (one food item in actor's tray, one in recipient's tray); 2) 0-1 (no food items in actor's tray, one in recipient's tray); 3) 1-0 (one food item in actor's tray, no food items in recipient's tray). Trials were randomized within mixed solo sessions with the constraint that there could not be more than two of the same trial type in a row. Subjects had to pull "correctly" on 12/12 trials in order to proceed to the weighted mixed solo session. Pulling correctly meant pulling on all 1v1 and 1v0 trials while inhibiting pulling on all 0v1 trials. Subjects were expected to inhibit on the 0v1 trials because they were unable to access the food in adjacent compartment of the apparatus. Once subjects had reached the criterion of 12/12 correct pulls on the non-weighted mixed solo session they proceeded to the weighted mixed solo session. After reaching the criterion of 12/12 correct pulls on the weighted mixed solo session, actors proceeded to experimental sessions.

Procedure

Subjects were moved out of their home cages and into transport cages using small pieces of raisin. Subjects were then brought into the testing room. Once in the testing room, subjects were weighed while in transport cages. Transport cages were later weighed so that subjects' body weights could be calculated. Subjects were then moved from transport

cages into the apparatus again using small pieces of raisin. Once in the apparatus, subjects were given a few minutes to acclimate to the testing room before test trials commenced.

On each trial, the experimenter distributed food rewards to the recipient and actor trays using the following method. A single piece of food was held between the experimenter's index finger and thumb. The food item was presented in the actor's field of view and then placed in one of the trays. The recipient's rewards were always distributed first to ensure that actor's paid attention to the overall reward distribution (otherwise, an actor may have fixated on the reward in his/her dish). Once food items had been distributed, the experimenter opened actor and recipient doors simultaneously using remote switches. The experimenter then silently counted out four seconds. A timer was affixed to the apparatus to facilitate counting. If a subject pulled the tool within four seconds, the experimenter gave the actor and recipient as long as was needed to consume food items. If subjects became distracted before finishing all food items, the experimenter would lightly tap the food dishes to bring subjects' attention back to the food. In a few cases, recipients did not finish his/her food items. In these cases, the experimenter discreetly removed the recipient's uneaten items. If the actor failed to pull the tool within four seconds, the experimenter would close both doors simultaneously and remove each of the uneaten food items one by one, starting with the food items in the recipient's tray.

Coding and dependent variables

All sessions were videotaped. A research assistant (L. Stone), who was blind to hypotheses and unfamiliar with cotton-top tamarins, coded the videos of all experimental

sessions. Videos were coded in order to assess subjects' reaction times on each trial. Reaction time was measured from the moment the apparatus doors opened to the moment the subject grabbed the tool. Importantly, we were interested in time-to-grab as opposed to pulling time since the high inter-individual variation in weights would likely have resulted in high variation in pull times. The resulting reaction time was used as a proxy for subjects' decision-making time.

A random subset of 24 sessions (20% of total) was then re-coded by a second coder (NS) for reliability. Reaction time codes between the two coders were highly correlated (Pearson's correlation $r(250) = 0.97$). The discrepancy between coders time codes was not significantly different from zero (paired t-test, $t(251) = 1.0651$, $P = 0.288$, mean difference = 0.01 seconds).

Subject pulling (pull or no pull) was live-coded by the experimenter during sessions. Reaction time coding was then used to assess the reliability of live coding. To this end, video and live coder's data were put into three categories: 1) pull; 2) no pull, 3) other. The other category included cases where coders were unable to assess the precise timing of the subject's grab of the tool, where they considered the pull to be ambiguous or where one coder coded a trial that the other didn't code (e.g. when the experimenter accidentally ran a 13^{th} trial). Reliability between video and live coders was high (Cohen's kappa = 0.853; percent agreement = 97.25%).

Analyses

All statistical analyses were conducted using R statistical software (version 2.15.2, R Foundation for Statistical Computing, 2012). Subject tool pulling was analyzed using

Generalized Linear Mixed Models (GLMMs) with a binary response term (pull or no pull; Bolker et al., 2009). Reaction time data were log transformed and analyzed using Linear Mixed Models (LMMs), as the transformed response term had a normal error distribution. To control for repeated measures, subject identity and trial number were included in mixed models as random factors (trial number was nested in subject identity). Mixed models were also used to test for trial effects. In these models, trial was included as a continuous predictor variable and subject identity as a random factor. All mixed models were run using R package lme4 (Bates et al., 2012).

We recognize that the use of mixed models for a sample size of seven is unconventional. We chose this method because results from more conventional nonparametric tests (e.g. rank-based ANOVAs) are dependent on how different methods account for ties in ranks. Given the high number of ties in our data (see Appendix 1, Table A1.2), results from rank-based procedures would thus not have been a robust means of analyzing our data. Given the limitations of rank-based analyses, we chose to use mixed models which would allow us to (a) control for repeated measures (b) analyze a nonlinear response term. Due to our small sample size, however, our models have low power. We have thus been suitably cautious in our conclusions from these analyses.

In mixed model analyses, we first examined a null model, which included only subject identity and trial number. We then the compared the null model to a full model that included condition as a three-level fixed factor. Model comparisons were conducted with likelihood ratio tests (LRT) using the 'anova' command in R. In cases where we found a significant effect of condition, Bonferroni-corrected Tukey's post-hoc tests were conducted using the 'multcomp' package (Hothorn et al., 2008).

Binomial tests were used to investigate whether subjects pulled the tool more than would have been expected by chance. For these analyses chance was set at 0.5 and all tests were two-tailed. Alpha was set at 0.05 for all statistical analyses. All figures show raw data and were created using the 'ggplot2' package (Wickham, 2009).

RESULTS

Decisions

Subjects' pulls across conditions are shown in Fig. 3.3. Subjects pulled the tool on almost all trials (total mean = 11.49 ± 1.26 out of 12 trials; 96% of all trials; see Appendix 1, Table A1.2 for raw data). Inspection of Fig. 3.3 shows that, although there was between-individual variation in rates of pulling, all subjects pulled more than would have been expected by chance (binomial tests on each subjects' total pulling, Ps < 0.001). Thus, all subjects tested in this study tended to pull the tool despite the fact that the reward that their pulling delivered for themselves was smaller (one item) than the reward for their partner (four items).

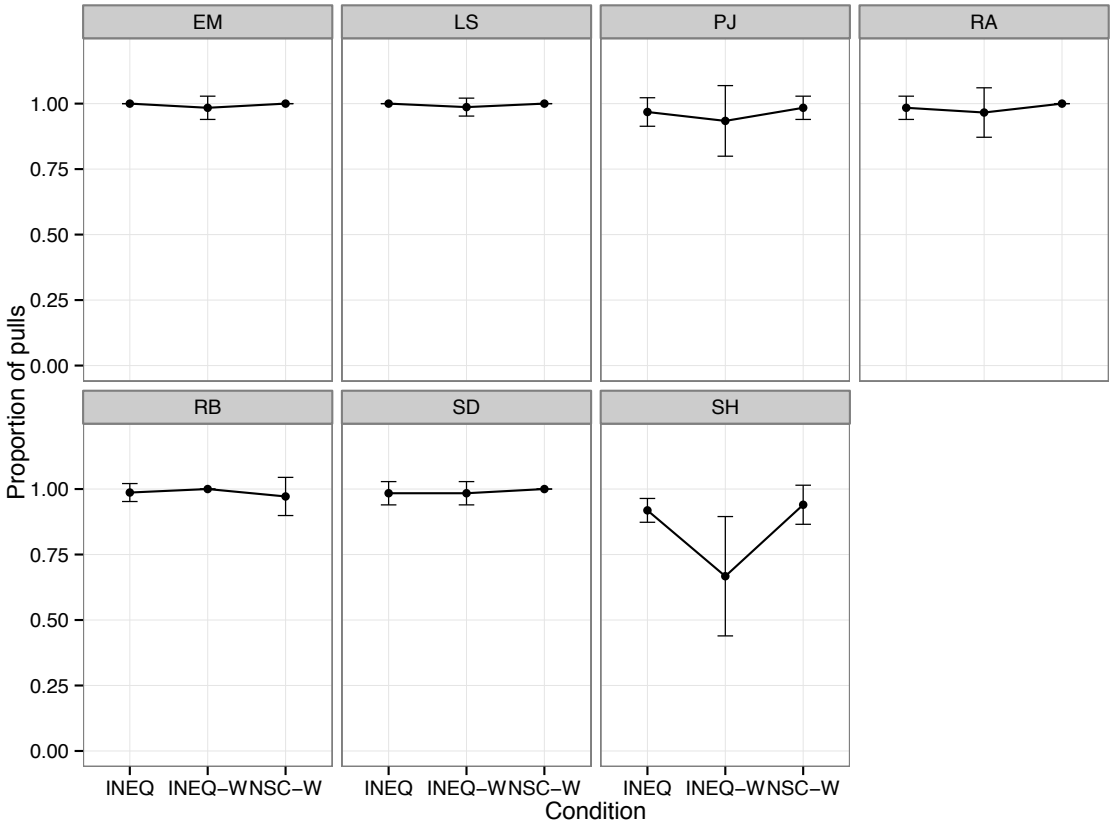

Figure 3.3. Line graph showing proportion of tool by condition for each subject. Conditions were as follows: 1) Inequity (INEQ), actor received 1 piece of food, recipient received 4 pieced of food and the tool was not weighted; 2) Weighted Inequity (INEQ-W), actor received one piece of food, recipient received four pieces of food and a weight was attached to the tool; Weighted Non-social Control (NSC-W), actor receives one piece of food, while four pieces of food are placed on absent recipient's tray and a weight is attached to the tool. Error bars show 95% confidence intervals.

Subjects pulled the tool on almost all trials across conditions. On average, subjects pulled on 11.79 trials (sd = 0.57) in the NSC-W condition, on 11.62 trials (sd = 0.59) in the INEQ condition and on 11.05 trials (sd = 1.96) in the INEQ-W condition. Levels of pulling for each subject in each condition were above chance (binomial tests on each subjects' total pulling in each condition, *P*s > 0.003). Thus, subjects were willing to

pull the tool to deliver an inequitable payoff on almost all trials even when pulling was effortful.

Despite the overall high levels of pulling across conditions, subjects' propensities to pull did vary slightly by condition. Five out of seven subjects were less likely to pull in the INEQ-W condition compared to the other two conditions (Fig. 3.3). One subject was least likely to pull in the INEQ condition (SD). One subject was least likely to pull in the NSC-W condition (RB). We assumed that subjects had an equal probability of exhibiting their lowest rate of pulling in any of the three conditions. In other words, we assumed that the probability that a subject would exhibit his/her lowest rate of pulling in any one of the three conditions was one-third. If this assumption is correct then the observed distribution of five out of seven subjects who pulled least in INEQ-W was not significantly different from chance ($X^2_2 = 4.57$, $P = 0.102$).

However, a GLMM with pulls (yes/no) set as the response term and condition as the predictor variable showed that condition was a significant predictor of subjects' pulling (LRT, $X^2_2 = 30.54$, $P < 0.001$; see Appendix 1, Table A1.3) for null and minimal model output). Bonferroni-corrected Tukey's post-hoc tests showed that the probability of pulling differed significantly between INEQ and INEQ-W ($z = -3.83$, $P < 0.001$) and between INEQ-W and NSC-W ($z = 4.4$, $P < 0.001$) but not between INEQ and NSC-W ($z = 0.94$, $P = 1$). This finding indicates that subjects were less likely to pull the tool when doing so was effortful and would deliver an unequal payoff to a partner. This effect could not have been due simply to effort since subjects pulled at similar levels in the NSC-W and the INEQ condition. Furthermore, this effect could not have been due simply to inequity since subjects pulled at higher levels in the INEQ condition compared to the

INEQ-W condition. Thus, subjects' slight drop in pulling was most likely the result of an interaction between inequity and effort.

Inspection of Fig. 3.3 shows that the effect of condition on pulling was most pronounced in one subject (SH). SH's pulling dropped markedly in the INEQ-W compared to the other conditions. In other subjects, the slight drop in pulling in INEQ-W was the result of a small decrease in pulls (sometimes only one non-pull trial; Appendix1, Table A1.2). Thus, while there was an overall effect of condition on pulling in our study, it was only clearly exhibited by one individual.

Reaction time

Fig. 3.4 shows reaction times by subject and condition. Subjects were quick to pull the tool when the gate was opened. On average, they pulled the tool about half a second after doors opened (mean = 0.51 ± sd = 0.79 s). Subjects' reaction times tended to be fastest in the INEQ condition (INEQ = 0.44 ± 0.5), slower in the INEQ-W condition (0.50 ± 0.68), and slowest in the NSC-W condition (0.59 ± 1.06 s). Additionally, as Fig. 3.4 shows, there was a striking degree of inter-individual variation across subjects. For example, SH (the subject who pulled the least overall), tended to wait longer to pull the tool than other subjects across the three conditions, suggesting that she was taking longer to decide her action.

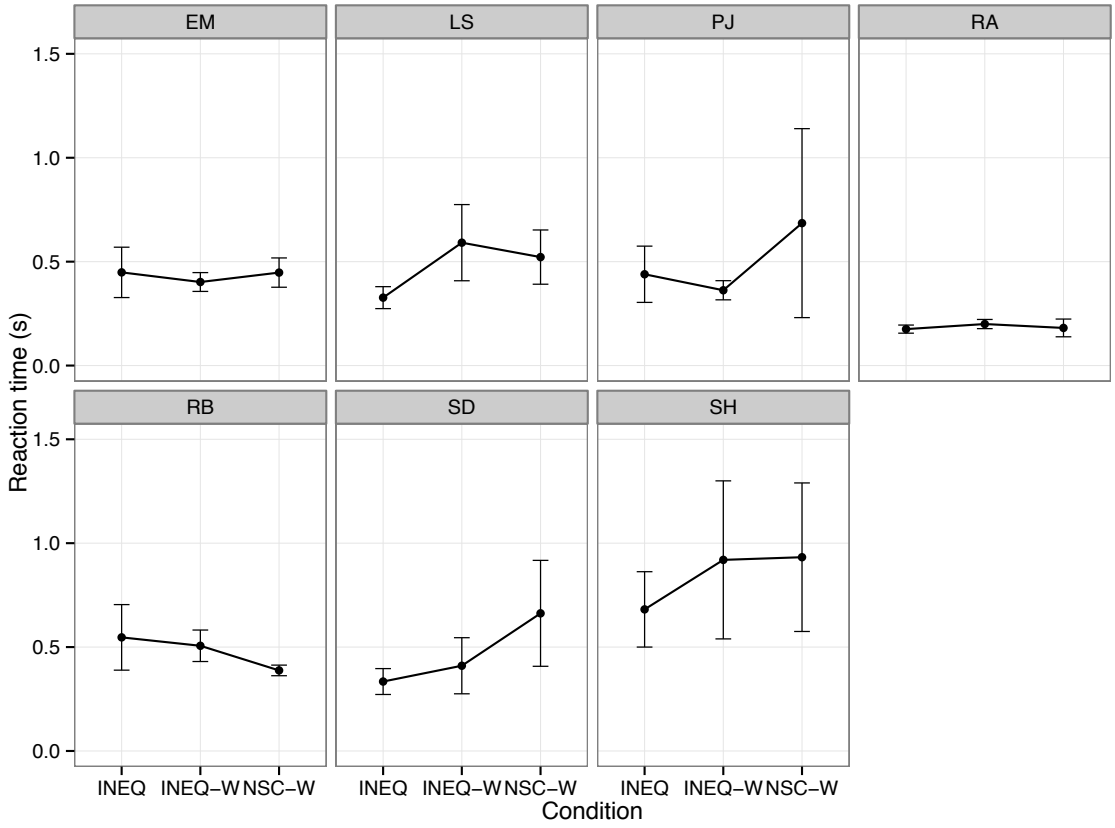

Figure 3.4. Line graph showing reaction time (time between gate opening and the initiation of a tool pull) by condition for each subject. Conditions were as follows: 1) Inequity (INEQ), actor received 1 piece of food, recipient received 4 pieced of food and the tool was not weighted; 2) Weighted Inequity (INEQ-W), actor received one piece of food, recipient reveived four pieces of food and a weight was attached to the tool; Weighted Non-social Control (NSC-W), actor receives one piece of food, while four pieces of food are placed on absent recipient's tray and a weight is attached to the tool. Error bars show 95% confidence intervals.

To test whether reaction times varied across condition, we ran a LMM with logged reaction time as the response term and condition as the predictor variable. The inclusion of the condition term significantly improved the model fit compared to the null model (LRT, $X^2_2 = 6.33$, $P = 0.04$; see Appendix 1, Table A1.3 for null and minimal model output). Coefficients from the minimal model ($\beta = 0.09$ for both INEQ-W and NSC-W relative to INEQ) suggest that subjects were slower to react on the two weighted conditions compared to the non-weighted condition. However, these effects were small. A back-transformation of these effects showed that subjects were approximately 0.03 s slower to react in the weighted conditions compared to the non-weighted conditions. Furthermore, bonferroni-corrected Tukey's post-hoc tests showed that reaction times were only marginally different between INEQ-W and INEQ ($z = 2.17$, $P = 0.09$) and between NSC-w and INEQ ($z = 2.22$, $P = 0.08$) and were not different between NSC-W and INEQ-W ($z = 0.06$, $P = 1$).

In sum, subjects' were quick to pull the tool across all conditions. However, they were slightly slower to react in the two weighted conditions compared to the non-weighted condition. This finding suggests that subjects were marginally more reluctant to pull the tool when pulling was effortful.

Trial effects

In the above analyses, we controlled for trial effects by nesting trial within subject identity and including this nested term as a random effect in mixed models. However, we were also interested in whether subjects' tendencies to pull and their reaction times

changed across the 12 experimental trials. Fig. 3.5 shows subjects' pulls (A) and reaction times (B) across trials. Inspection of this figure shows that subjects were less likely to pull in the early trials compared to the later trials. Furthermore, this figure shows that subjects' reaction times decreased over trials. Indeed, a GLMM of subject's pulls in relation to trial showed that trial number was a significant predictor or pulling (LRT, $X^2_1 = 38.23$, $P < 0.001$). Similarly, a LMM of logged reaction time in relation to trial showed that trial was again a significant predictor (LRT, $X^2_1 = 11.60$, $P < 0.001$). Thus, subjects were more likely to pull and faster to pull with increasing trial number. Due to our limited sample size, we were unable to examine the interaction between condition and trial number (see Appendix 1, Fig. A1.2 for trial effects by condition).

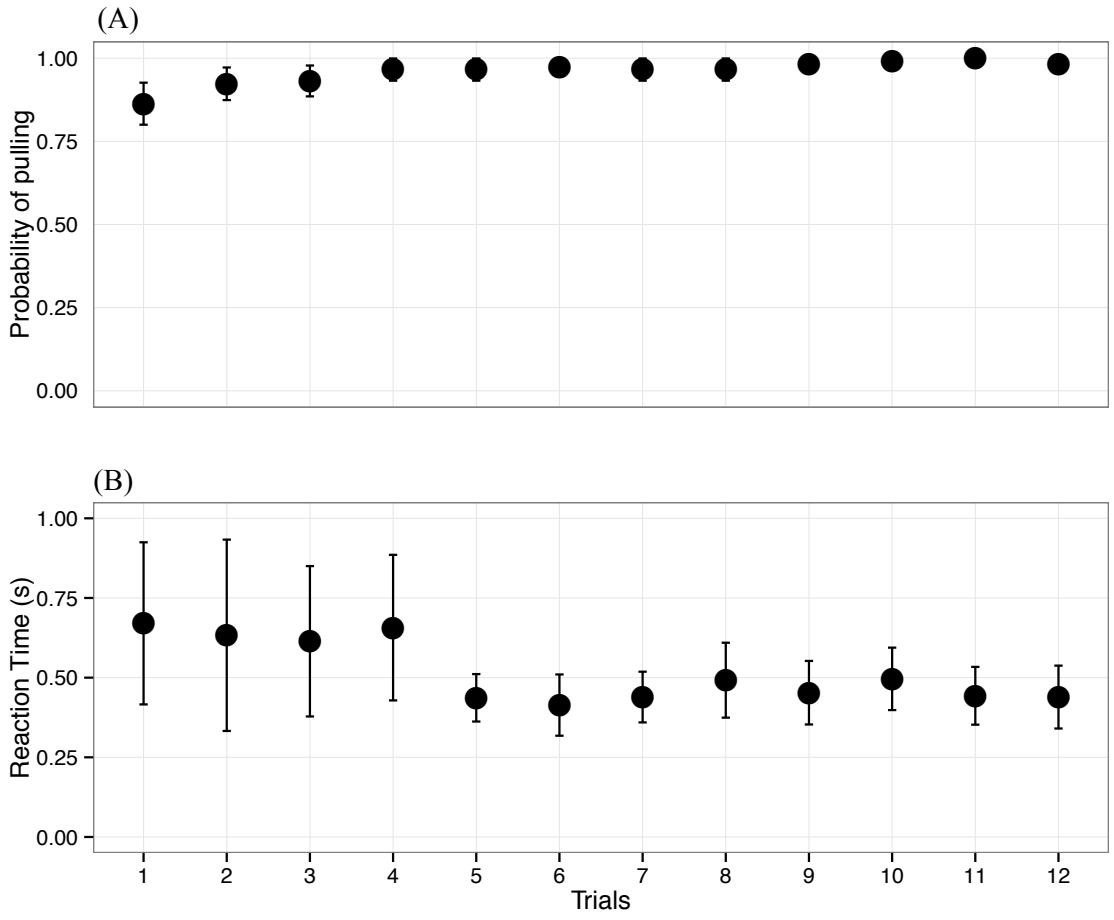

Figure 3.5. Line graph showing the probability of pulling the tool (A) and reaction time (B; time between gate opening and the initiation of a tool pull) across trials. Error bars show 95% confidence intervals.

DISCUSSION

Our main question was whether cotton-top tamarins would show an increased aversion to inequity when the acceptance of an unequal reward distribution was effortful compared to when it was effortless. Additionally, we were interested in whether a heightened response to inequity in the face of effort was specific to cases where a partner was present or whether it was common both to social and nonsocial contexts.

We found weak support for the influence of effort on inequity aversion. Subjects were less likely to accept (i.e. pull) an unequal reward allocation in the weighted inequity condition (INEQ-W) compared to the weighted nonsocial control (NSC-W) or the non-weighted inequity (INEQ) condition. While five out of seven subjects showed an effect of condition in this direction, the effect was only pronounced in one individual. In the other four individuals the effect of condition was very small, in two cases even resulting from a single missed pull amongst hundreds of trials. The female SH, however, showed a strong effect of condition. Her rate of pulling dropped markedly in the INEQ-W condition compared to the other two conditions.

In this way, our findings are inconclusive but leave open the possibility that subjects were not solely focused on the inequality of outcomes. Our results show that one individual's behavior was clearly sensitive to the effort required to accept unequal outcomes, while in four of the remaining 6 individuals there was a suggestion that the same capacity was found. If subjects had been focused solely on unequal outcomes then their rejections (i.e. inhibited pulls) should have been the same across experimental conditions. Furthermore, the finding that subjects were less likely to pull the tool in the weighted inequity condition compared to the nonsocial weighted condition indicates that subjects were not simply averse to exerting effort for an unequal reward distribution (that delivered an inaccessible high value reward). Instead, their responses to inequality were strongest (although still weak overall) in the condition where they had to exert effort to accept inequality when paired with a recipient. We tentatively suggest that this result is more consistent with the idea that subjects were guided by a process analogous to the human principle of equity than by a process analogous the human principle of equality.

By this we mean that subjects were sensitive to the relationship between effort and reward distribution as opposed to the inequality of the reward distribution alone. We do not suggest that subjects in our task were acting on an internal representation of equity but rather that they were capable of an evolved or developed response to violations of equity.

If cotton top tamarins are truly sensitive to equity then we predict that they would also show sensitivity to inequities of effort when payoffs are equal. This result is observed in humans, including in young children (Adams, 1965; Baumard et al., 2012; Damon, 1977; Hook & Cook, 1979; Kanngiesser & Warneken, 2012; Sloane et al., 2012). Future work could thus extend our findings by asking whether cotton-top tamarins would be willing to exert unequal effort to accept an equitable payoff distribution (e.g. one food item for each subject). To our knowledge, no study of nonhuman animal inequity aversion has addressed this question by properly manipulating effort.

Our finding that effort had a marginal influence on tamarins' inequity aversion is broadly consistent with work on other nonhuman primates that shows that subjects show sensitivity not just to inequity but also to the effort-to-payoff ratio. For example, both Brosnan and de Waal (2003) and van Wolkenten et al., (2007) found that capuchin monkey subjects were least likely to trade tokens for low value food items when their partners received high valued items without having to trade. Additionally, a study of cotton-top tamarins found that individuals within a single colony differed in their reaction to inequity across two experiments: one that required a task (putting a token in a cup) and one that did not (Neiworth et al., 2009). Tamarins in their study showed an inequity aversion response only when engaging in the task and not when unequal reward

distributions were simply presented. Such findings have been used as support for the argument that the inequity aversion response evolved as a means of tracking the ratio of effort-to-payoff in cooperation activities and not simply as a means of tracking relative reward distributions (Brosnan, 2006; 2011; Dindo and de Waal, 2007).

While our results are compatible with the idea that inequity aversion evolved to allow individuals to regulate relative efforts and payoffs, we hesitate to draw strong conclusions from our study for three reasons. First, a potential alternative explanation for the observed drop in pulling in the INEQ-W condition compared to the other conditions is distraction. It is possible that subjects were more distracted when confronted with weight, inequity and a social partner (INEQ-W) compared to when confronted only with weight and inequity (NSC-W) or a partner and inequity (INEQ). While we do not think that distraction was an important factor in our task given the high levels of pulling overall and the short reaction times (which suggest that tamarins were attentive and motivated in our task) we cannot presently rule out the potential effects of distraction. Also, note that - with one exception (Raihani et al., 2012) - past work on inequity aversion in nonhuman animals has not addressed distraction as a possible confound. We thus suggest that future work on inequity aversion in nonhuman animals could include a "distraction control" where subjects are given unequal reward distribution in the absence of a partner but in the presence of a nearby conspecific. This control would allow for distraction to be held constant between social inequity conditions and nonsocial control conditions.

Second, a striking finding from our study is the degree to which individuals differed in their responses to experimental conditions. Individual SH was the only subject in our study who showed a strong response to the weighted inequity condition. Given the

weak effects seen across other individuals, it is clear that SH's response contributed greatly to the main effect of condition in our model. Indeed, although mixed models control for inter-individual variation, they may be sensitive to extreme observations. Given the high inter-individual variation and our small sample size, we are reluctant to claim that these results are likely to be common to cotton-top tamarins as a species. We suspect that inter-individual differences in inequity responses are common in experiments like ours that test a small number of subjects. However, individual responses to inequity are seldom reported (Brosnan and de Waal, 2003; Neiworth et al., 2009; van Wolkenten et al., 2007). Our findings suggest that it is of paramount importance to report inter-individual variation in inequity aversion tasks because such variation may be important to explaining overall effects. Additionally, understanding the extent to which individuals vary in their responses to inequity could help us make sense of the inconsistent results between different inequity aversion studies.

Third, although condition affected subjects' pulling in this task, overall rates of pulling were almost at ceiling across all conditions (on average, subjects pulled on 11 out of 12 trials). Even SH, who showed the strongest response to condition, continued to exert effort in order to accept unequal offers at a higher rate than would have been expected by chance. We are thus doubtful that the strength of the effect of condition demonstrated in our study is biologically meaningful. It is possible that our task tapped a latent capacity to identify and avoid inequitable situations. It is also possible this capacity could be beneficial to cooperative cotton-top tamarins in the wild (Cronin et al., 2008; Neiworth et al., 2009). However, if the ability to forgo an inequitable payoff distribution even at personal cost confers a selective benefit to tamarins, then one would expect this

capacity to be most readily expressed in the relative luxury of a captive environment where individuals do not face resource constraints.

In line with the finding that subjects readily accepted unequal resource distributions across conditions is the result that subjects' were quick to make decisions in this task. Subjects' reaction times did, however, vary across conditions: they were slower to pull the tool in the two weighted conditions (INEQ-W and NSC-W) compared to the non-weighted condition (INEQ). This result most likely indicates that subjects were less motivated to pull the tool when it was difficult to pull than when it was easy to pull.

We observed an interesting pattern of pulling and reaction time over the 12 experimental trials. Subjects were more likely to pull the tool, and were quicker to pull the tool as trial number increased. In other words, subjects were slightly less motivated to accept an unequal reward allocation in the early trials. This finding could indicate that subjects more readily expressed their true aversion to inequity when they were first confronted with it. As the session progressed, subjects became habituated to the unequal reward distribution and were thus less likely to reject it. Indeed, studies of human adults typically avoid repeated trials and instead focus on subject's one-shot (or spontaneous) response to different payoff distributions (e.g. Güth et al., 1982). However, another possibility is that subjects became more comfortable in the testing set-up as the session progressed which would also explain their increased probability of pulling and decreased reaction time.

A possible limitation of our task is that we cannot be certain that subjects understood that pulling the tool (i.e. "accepting" a reward distribution) delivered food to another individual. In our pretest sessions (the 'mixed solo' sessions) we ensured that

subjects attended to the relative distribution of rewards between their own food dish and the recipient's. In these sessions, subjects had to inhibit pulling on any trials where no food items were placed in their dish. We thus ensured that subjects had not developed a simple rule of them whereby they indiscriminately pulled the tool. We further facilitated subjects' understanding of the task by always placing food in the recipient's dish first and ensuring that the subject paid attention to each piece of food as it was being delivered. We are therefore confident that subjects attended to overall reward distribution in experimental trials. Despite these precautions, it is still possible that subjects did not understand the causal contingency between pulling the tool and their partner receiving food. We suspect that subjects did understand this because past work on the same colony of tamarins showed that subjects understood a contingency between tool-pulling and reward distribution in a similar task (Hauser et al., 2003). Furthermore, our result demonstrating that subjects were more likely to pull in the NSC-W condition compared to the INEQ-W condition suggests that they understood that their actions delivered food to their partner. However, we have no data to confirm their understanding of this contingency and recognize this as a potential limitation of our design.

In our view, the most notable contribution of the present study is a methodological one. A limitation of past work that has addressed the influence of effort on inequity aversion is that effort has not been measured directly. Instead, the inclusion of any task (e.g. trading a token) was considered to have involved effort (Brosnan and de Waal, 2003; Neiworth et al., 2009; van Wolkenten et al., 2007). To our knowledge, the only study that indirectly manipulated effort is van Wolkenten et al.'s (2007), in which effort was varied by arranging for subjects to trade three tokens in a "large effort"

condition and one token in an "small effort" condition. Even with this method, however, it is not clear that subjects perceived trading three tokens as effortful.

Previous methods for testing effort have been buttressed by two critical assumptions: 1) subjects perceive any task as effortful and 2) effort is perceived uniformly across subjects. Our study indicates that neither of these assumptions is justified. During weights training for our study we increased weights until subjects were no longer willing to consistently pull the tool. In doing so, we ensured that the task was perceived as effortful to each individual. Furthermore, subjects in our study showed marked variation in the amount of weight that they were willing to pull. This method allowed for the successful calibration of effort to each subject and thus provided a much stronger test of the relationship between effort and inequity than was previously possible.

In sum, we found weak evidence for the influence of effort on inequity aversion. Given the weakness of the observed effect and our small sample, we are reluctant to make species-level claims about the relationship between inequity aversion and effort in cotton-top tamarins but view this as a fruitful area of future inquiry. Specifically, studies of tamarins' responses to equality resulting from an inequality of effort could enhance our understanding of constraints on their response to inequity. We further suggest that future work on inequity aversion in nonhuman animals should focus on characterizing inter-individual responses to inequity. Such work should include proper calibration of work effort to individual abilities. Finally, we argue that it is critical to be cautious when extrapolating conclusions about inequity aversion from test subjects to species.

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CHAPTER 4

INEQUITY AVERSION IN SOCIAL CANIDS: A COMPARISON BETWEEN DOMESTIC DOGS (*CANIS FAMILIARIS*) AND DINGOES (*CANIS DINGO*)

INTRODUCTION

Cooperation, where one individual provides a benefit to another individual (West et al., 2007), is vulnerable to exploitation by defectors, agents who benefit from cooperative action without investing in cooperation. Humans avoid exploitation by defectors partly by paying close attention to how the spoils of collective action are distributed and by punishing individuals who take more than their fair share (Fehr & Fischbacher, 2004; Fehr & Gächter, 2000; Fehr & Schmidt, 1999; Raihani & McAuliffe, 2012b). Indeed, a large body of research has demonstrated that human adults exhibit a strong aversion to unfair outcomes and are often willing to sacrifice personal resources to avoid receiving relatively more than a peer (advantageous inequity) or relatively less than a peer (disadvantageous inequity; Camerer, 2003; Dawes et al., 2007; Güth et al., 1982; Loewenstein et al., 1989). This aversion to unequal outcomes – or inequity aversion - is considered to be an important psychological mechanism that contributes to the persistence of cooperation among unrelated individuals (Brosnan, 2006, 2011; Fehr & Schmidt, 1999).

While inequity aversion is thought to be an integral component of human cooperation, the extent to which inequity aversion promotes cooperation in nonhuman species remains poorly understood (Chen and Santos, 2006). Recent years have seen the

emergence of a number of nonhuman animal (hereafter 'animal') studies that aimed to investigate the evolutionary roots of inequity aversion. With two exceptions (Brosnan et al., 2005; Horowitz, 2012), work on animal inequity aversion has focused on whether animals express an aversion to disadvantageous inequity as opposed to advantageous inequity.

Inequity aversion in nonhuman species

Brosnan and de Waal (2003) conducted the first experimental test of disadvantageous inequity aversion (hereafter, 'inequity aversion') in a nonhuman primate by asking whether captive brown capuchins (*Cebus apella*) would refuse to participate in a task where they received a lower payoff than an adjacent individual (partner) for exerting the same effort. In their experiment, two monkeys were placed in adjacent cages and prompted to trade a token for a food reward. In the "equity" condition, both the subject and partner traded tokens for pieces of cucumber, a low value reward. In the "inequity" condition, the partner received a highly valued grape in return for her token while the subject continued to receive a piece of cucumber. Brosnan and de Waal compared these two conditions to two controls. First, an "effort control" was conducted, where the partner received a grape without having to trade a token while the subject received a piece of cucumber. In other words, the partner was given a grape for free while the subject had to "work" for a cucumber. Second, a "food control" was conducted, where a grape was placed in an empty cage adjacent to the subject and the subject was prompted to trade for a cucumber. In this control, the subject could see, but could not access, the high value grape. Results showed that capuchin monkeys consistently traded tokens in

the equity condition but were less likely to trade in the other conditions. Capuchins were least likely to trade in the effort control, indicating that they were attending both to relative effort as well as to relative payoffs. Brosnan and de Waal interpreted their findings as the first evidence for inequity aversion in an animal species and suggested that inequity aversion has deep evolutionary roots.

A number of studies have followed up on Brosnan and de Waal's experiment (Dubreuil et al., 2006; Roma et al., 2006; Silberberg et al., 2009; van Wolkenten et al., 2007). Some have provided further support for the claim that inequity aversion has deep evolutionary roots and is expressed by nonhuman primates (capuchins: Fletcher, 2008; van Wolkenten et al., 2007; chimpanzees (*Pan troglodytes*): Brosnan et al. 2005; cotton-top tamarins (*Saguinus oedipus*): Neiworth et al., 2009). Others have found that what appears to be inequity aversion in primates can be explained by nonsocial factors such as frustration at not being able to access a highly valued food reward when it is present or when it has been available in the past (capuchins: Dubreuil et al., 2006; Roma et al., 2006; Silberberg et al., 2009; chimpanzees: Brauer et al., 2006, 2009).

Given these mixed results, we currently do not know whether the expression of inequity aversion in captive experiments is an artifact of different experimental designs or whether inequity aversion occurs in nonhuman primate societies at all. Nevertheless, an intriguing pattern has emerged. Studies that have provided putative support for inequity aversion in nonhuman primates have tested species that are considered to be cooperative (capuchins: Fletcher, 2008; van Wolkenten, et al., 2007; chimpanzees: Brosnan et al. 2005; cotton-top tamarins: Neiworth et al., 2009). In contrast, studies of primate species that are not considered to be cooperative have shown no support for inequity aversion

(orangutans (*Pongo pygmaeus*): Brosnan et al., 2011; squirrel monkeys (*Saimiri sciureus* and *Saimiri boliviensis*): Talbot et al., 2011).

As a way to make progress in understanding whether inequity aversion is indeed associated with an evolutionary history of cooperation, several studies have tested non-primate species that are especially cooperative (domestic dogs, hereafter 'dogs' (*Canis familiaris*): Horowitz, 2012; Range et al., 2009; Range et al., 2012), cleaner fish (*Labroides dimidiatus*): Raihani & McAuliffe, 2012a; Raihani et al., 2012). Dogs are an ideal model species for studies of inequity aversion because they cooperate extensively both with conspecifics and humans (reviewed in Range et al., 2012; Miklósi, 2007). Dogs appear to have evolved from a wolf ancestor (e.g. Arabian sub-species of *Canis lupus*) that presumably routinely hunted cooperatively and engaged in cooperative food sharing as extant wolves do (Peterson & Ciucci, 2003; Miklósi, 2007). Sensitivity to the distribution of food resources in relation to labor is therefore expected to be a useful trait. After domestication[2], dogs became reliant on humans for food. Because of this newfound reliance, dogs may have become sensitive to the distribution of food from a human experimenter. This means that the experimental paradigm used to test inequity aversion may be less artificial for dogs than for non-domesticated species, suggesting that if dogs have the capacity for inequity aversion, it should be easily detectable.

Inequity aversion in dogs

Range and colleagues (2009) conducted the first experimental test of inequity aversion in dogs. Their study resembled the Brosnan and de Waal (2003) experiment, except that

[2] Following Price (1984), domestication is defined here as involving: "adaptation to man and the environment he provides … achieved through some combination of genetic change over generations and of environmental influences and experiences during an animal's lifetime."

instead of trading tokens, subjects were asked to "give paw" to an experimenter in order to receive a reward. "Giving paw" means that, upon hearing the command "give paw", the dog had to extend a paw to meet an experimenter's hand. They tested pairs of familiar dogs on four test conditions: 1) "equity", where both dogs received a low value piece of food (bread) in return for giving paw; 2) "quality inequity", where the subject dog received bread for giving paw while its partner received a high value item (sausage); 3) "reward inequity", where the subject received no reward for giving paw while its partner received bread; 4) "effort control", where the subject received bread for giving paw and its partner received bread for doing nothing. These test conditions were then compared to a non-social, "no reward control" condition, where subjects were tested without a partner and asked to give paw for no reward. Range et al. found that dogs refused to give paw more in the reward inequity condition than any of the other conditions, including the non-social control. Thus, dogs in their study showed sensitivity in the social condition to the absence of a reward but, interestingly, not to differences in reward value (quality inequity condition) or effort exerted in the task (effort control).

Range et al.'s finding that dogs were sensitive to reward inequity is consistent with the idea that because dogs evolved from a cooperative ancestor, they exhibit mechanism for tracking relative payoffs from joint action. However, inequity aversion in dogs in also consistent with an alternative hypothesis that inequity aversion in dogs is the product of domestication by humans. It is possible that the human-dog relationship that developed over the course of dog domestication means that dogs pay close attention to how they are being treated by humans relative to conspecifics. If inequity aversion in dogs is due to domestication then we would expect to see inequity aversion only in dogs

and not in other closely related, non-domesticated, social canid species. If, on the other hand, inequity aversion evolved as a response to the demands of intraspecific cooperation, then we would expect other cooperative canids to show inequity aversion as well.

Current study

In the present study I aim to distinguish between these two hypotheses for the expression of inequity aversion in dogs by testing dogs and a closely related species, the dingo (*Canis dingo*), on the same inequity aversion task. Dingoes are a well-suited comparative species because they are closely related to dogs and show intraspecific cooperation in the wild. Critically, extant dingoes are not considered to be a domesticated species (Corbett, 1995; Miklósi, 2007; Smith, 2010). The extent to which dingoes ever were domesticated is a controversial subject (see Smith, 2010 for a review). However, it is generally accepted that dingoes differ markedly from dogs in their behavior, physiology and cognition (Corbett, 1995; Smith, 2010). Thus, dingoes offer a unique opportunity to study inequity aversion in a closely related but non-domesticated cooperative species.

The logic of the dog-to-dingo comparison in the present study is as follows: if inequity aversion evolved for cooperation in social canids, both dingoes and dogs should exhibit inequity aversion. If, on the other hand, inequity aversion evolved as a product of domestication by humans then dogs, but not dingoes, should show inequity aversion. If neither species shows inequity aversion, we would have evidence suggesting that the expression of inequity aversion is not a robust feature of social canid cognition.

In designing a task that could distinguish between the two alternative hypotheses for the evolution of inequity aversion in dogs it was important to control for two key

aspects of the experimental design that could have importantly influenced subjects' behavior: 1) the relationship between subjects; 2) the distribution of food rewards.

First, this study paired subjects with an unfamiliar conspecific. This sort of design differs from Range et al. (2009), in which dogs were tested in familiar pairs. Because pairs were familiar it is difficult to know whether dogs were intolerant of inequity only when it occurs in the context of an ongoing relationship or whether it is a more general feature of dog social cognition. Indeed, Range et al. (2012) explored the importance of the subject-partner relationship in a follow-up study and suggest that a high quality relationship between dogs may indeed make individuals less tolerance of unequal reward allocations. What is not clear, however, is whether inequity aversion in dogs is specific to familiar individuals or whether it is a more general trait. Parallel work on human inequity aversion can clearly highlights the importance of relationships but in a contrasting direction. In humans, individuals in close relationships are unlikely to show an aversion to inequity (Clark & Grote, 2003; Fiske, 1992). It is thus surprising that dogs seem to show the opposite pattern: namely, increasing inequity aversion with increasing social closeness.

Given that the only evidence for inequity aversion in dogs comes from studies of familiar dogs, it is unclear whether inequity aversion is influenced by relationship quality or a direct consequence of relationship quality. A recent study on inequity aversion in dogs (Horowitz, 2012), addressed the possible confound of familiarity between subjects by testing all dogs with an unfamiliar confederate partner. In this study, I used this same method and tested both dingo and dog subjects with an unfamiliar confederate partner.

Second, the current study focused exclusively on reward inequity, where a subject receives no reward while his/her partner receives a reward (analogous to the Reward Inequity condition in Range et al. (2009). Note that Range et al (2009) found that dogs exhibited inequity aversion only in the context of reward inequity and did not exhibit inequity aversion when faced with inequities of quality or effort. Additionally, Horowitz (2012) recently tested whether dogs would exhibit inequity aversion in a task where both subject and partner were rewarded but where rewards were distributed inequitably. Findings from this study indicated that dogs were insensitive to inequity in this context. Because dogs only show inequity aversion when they get nothing and another dog gets a reward, the current study focused exclusively on this reward distribution.

Both dogs and dingoes tested in this study had extensive experience with humans before testing, which controls for potential species differences in apparent inequity aversion due to differing levels of comfort with human experimenters. However, dingoes differ markedly from dogs in their propensity to attend to humans (Smith & Litchfield, 2010). Thus, in order to test both dogs and dingoes in a comparable way, the current study designed an inequity task that would not require behaviors that are commonly trained in dogs but are absent in dingoes (e.g. "give paw"). Instead, subjects watched as the experimenter distributed food between two plates and then had the opportunity to approach the plates. This design feature had an additional strength of allowing subjects to see the overall distribution of food before making a decision about whether or not to participate in the task (i.e. to approach the plates). Simultaneous distribution of food is a departure from past studies of dog inequity aversion where food was distributed sequentially (Brosnan & de Waal, 2003; Brosnan et al., 2005). By contrast to the

"sequential" method, my method did not require subjects to remember what their partner received. In this respect, the current method was similar to methods of resource distribution used in studies of human adults (Güth et al., 1982) and children (Blake & McAuliffe, 2011) as well as in recent work on inequity aversion in animals (Raihani, et al., 2012).

If subjects are sensitive to inequity they should be less motivated to approach under conditions of reward inequity. Furthermore, if inequity aversion is common to cooperative canids, then both dogs and dingoes will show this effect. However, if inequity aversion in dogs is a product of domestication then these effects will only be observed in dog subjects.

In addition to investigating whether dogs and dingoes show differences in their propensity to approach plates in this task, the current study also explored whether are subjects differed in their latency to approach (i.e. reaction time) across conditions. Reaction time is a valuable measure because in the absence of obvious behaviors it can provide insight into subjects' decision-making processes (Blake & McAuliffe, 2011; Piovesan & Wengstrom, 2009). Finally, to understand whether dogs and dingoes perceive inequity as a social problem, I ask whether subjects show differences in their tendency to look at (i.e. "reference") humans in different experimental conditions (Miklósi et al., 2003; Smith, 2010).

METHOD

Subjects

Subjects were 72 dogs (47 females, 25 males) and 11 dingoes (8 females, 3 males). This discrepancy in sample size is due to differences in both (1) the availability of subjects and (2) subjects comfort-levels with an unfamiliar human (i.e. the experimenter).

Dogs were recruited and tested through the Canine Cognition Lab at Harvard University during October 2010 – May 2011 (see Appendix 2, Table A2.1 for subjects by sex and breed). Subjects were recruited by contacting dog owners in the greater Boston area. Before testing, owners were asked to complete an aggression questionnaire. Dogs that received a high aggression score were not permitted to enter the lab. No dogs recruited for this study had to be turned away due to a high aggression score. Following completion of the aggression questionnaire, owners were invited to bring their dog into the testing room where they were given instructions on how to handle their dog during the experiment.

Dingo subjects were recruited and tested at the Dingo Discovery and Research Center in Toolern Vale, Victoria, Australia during July and August 2010 (see Appendix 2, Table A2.2 for subjects by sex). All breeding lines at the sanctuary have been DNA tested for purity. Dingo subjects were selected based on their level of comfort with humans. Dingoes were housed in pairs in night pens of 30 square meters, with indoor/outdoor access. All dingoes were given regular access to exercise enclosures ranging from 400 square meters to 1500 square meters. Water was piped to automatic dispensers in each night pen, and to each exercise enclosure. Dingoes were fed a combination of high quality commercial dog food and meat once daily. Staff members at the Dingo Discovery and Research Center and a research assistant handled the dingoes in all experiments.

Both dogs and dingoes were tested with an unfamiliar confederate partner. Confederate partners for dog subjects were two dogs from the Harvard community. During testing, confederate partners were handled by research assistants. Before testing, the subject dog and the confederate partner were allowed to greet one another while on leashes to minimize the risk of aggression during the experiment. The confederate dingo partner was a female dingo living at the Sanctuary who was chosen to be the confederate a priori because she had not socialized with the other subjects. Immediately prior to dingo testing, the subject was walked past the confederate either in her home enclosure or in the testing arena, depending on which individual was brought into the testing area first.

Experimental set-up

Dogs were tested in a laboratory room (Fig. 4.1a). Prior to the experiment, the subject was brought into the testing area and given a few minutes to explore and habituate to the testing room. Once exploratory behavior ceased, the confederate partner was brought into the testing room and both dogs were attached to leashes that were connected to two chairs in opposite corners of the room. The subject and confederate handlers were instructed to sit in the chairs and to hold the dogs' leashes until the experimenter indicated that the dogs could be released (by signaling with a clear drop of the head). A large Plexiglas barrier separated the dogs. The experimenter stood at the barrier and placed food on two plates that were positioned on either side of the barrier. On the subject's side of the barrier, a large rectangular "approach box" was marked on the floor by black tape (approximately 4.5 x 3.5 feet).

(A)

(B)

Figure 4.1. Testing set-up for dogs (A) and dingoes (B). The subject's handler and subject sat on the right of a transparent barrier and the partner and the partner's handler sat on the left of the barrier. The experimenter stood in the middle of the testing space, called the subjects, and distributed rewards on plates. A subject was considered to have approached when he/she had two front paws in the box surrounding the plate (box marked by black tape for dogs and yellow cones and blue ribbon for dingoes).

The experimental set-up for the dingoes was equivalent to the dog set-up with the only major difference being that dingoes were tested in a fenced outdoor enclosure rather than in a laboratory (Fig. 4.1b). Dingoes were tested outside because the majority of dingo subjects were not accustomed to being indoors. All dimensions of the testing area were

identical for dog and dingo subjects but the approach box for the dingoes was marked on the ground by blue ribbon and yellow cones instead of black tape. This difference in marking was necessary because tape would not stick to the grass.

Research design

Before testing, subjects were given warm-up trials to ensure that they were comfortable approaching and eating from the plates. During warm-ups, both subject and confederate were called to the plates at the same time and given a reward (see procedure below). Subjects had to approach on two consecutive warm-up trials before they proceeded to the experiment. Warm-up trials additionally allowed me to ensure that handlers were reliably releasing subjects at the correct time (i.e. in response to the release cue).

After warm-up trials the experimental session began. Only one session was run per day. Each experimental session consisted of two halves. The first half of each session consisted of 15 "baseline" trials where both subject and confederate partner were given a food reward for approaching. Following baseline trials, subjects were given a short break and were offered water. In one case during dingo testing the water break was skipped due to inclement weather. Following the short break, 15 "test" trials were conducted. The distribution of rewards in test trials varied depending on condition as did whether or not the confederate partner was present (see Table 4.1 for a description of conditions). Regardless of condition, subjects never received a treat for approaching during test trials. Test trials were always preceded by baseline trials in order to control for the possibility that subjects would lose motivation over the course of a session: because non-rewarded

session halves always occurred after rewarded session halves, the potential effects of loss of motivation were consistent across all conditions.

Table 4.1. Description of conditions administered in the test half of sessions. Prior to the test half, subjects were tested in a baseline condition where, with one exception, both subject and partner were rewarded for approaching the plate. In the Non-Social Control 2 treatment, the baseline was run in the absence of a partner dog and thus food was simply placed on the partner's plate. Food was always absent from subjects' plates during tests.

	Condition	Description	Partner present during test?	Food on partner's plate?
Social	Inequity	Subject and partner are called to plates and only the partner is rewarded for approaching.	Yes	Yes
	Social No Reward	Subject and partner are called to plates and neither is rewarded for approaching	Yes	No
Non-Social	Non-Social Control 1	Subject is tested without partner and is called to plate but is not rewarded for approaching. Food is, however, placed on the partner's plate.	No	Yes
	Non-Social Control 2	Same as First Non-Social Control except that subject is tested in the baseline without a partner.	No	Yes
	Non-Social No Reward	Subject is tested without partner and is called to plate but is not rewarded for approaching. No food is placed on the partner's plate.	No	No

The main condition of interest was the *Inequity condition* (1). In this condition both subject and confederate partner were present and the confederate partner received a reward for approaching but the subject did not receive a reward for approaching. In addition to the Inequity condition, I administered four different control conditions.

A *Social Non Reinforced condition* (2) was used to control for the possibility that subjects may stop approaching in the Inequity condition because of frustration due to lack of food compounded with distraction by their partner rather than because of social inequity aversion per se. In the Social Non Reinforced condition, both the subject and

confederate partner were present but neither was rewarded for approaching. In order to ensure that the confederate partner approached during every trial, even on trials where no food had been placed on his/her plate, the experimenter secretly gave the confederate a treat at the end of each Social Non Reinforced trial, during the return to his handler. In addition, to control for the possibility that subjects may stop approaching in the Inequity condition because of frustration at not being able to access food on their partner's plate but not because their partner is getting the food, two non-social controls were conducted.

During both the *First* and *Second Non-social Control condition* (3, 4), the confederate partner was absent but food was placed on the confederate's plate. The only difference between these conditions was that during Second Non-social Control condition, the confederate partner was absent during baseline trials as well as during test trials and thus it was a completely non-social session. The logic of the Second Non-social Control condition condition was that completely removing the social component of the task while preserving the reward inequity might change subjects' propensity to participate in the task.

Finally, to understand whether subjects would be motivated to participate in the task in the absence of a partner and in the absence of a reward, a *Non-social Non Reinforced condition* (5) was run. In the Non-social Non Reinforced condition, the confederate partner was absent and no food was placed on either plate.

All five experimental conditions were run with both dog and dingo subjects. However, dogs were tested in a between-subject design while dingoes were tested in a within-subject design. This difference was due to the fact that dog owners could not bring their dogs to the lab on five different days. Consequently, each dog was tested on two

different days and was tested in the Inequity condition and one of the four control conditions. Thus dog subjects could be grouped into four different control groups (Social Non Reinforced, 19 dogs; First Non-social Control, 18 dogs; Second Non-social Control, 16 dogs; Non-social Non Reinforced, 19 dogs) within which subjects had been tested in the Inequity session and the associated control session. The order in which the inequity versus control sessions was administered was counterbalanced between dogs and within control groups (Appendix 2, Table A2.1). Dingo subjects, on the other hand, were each tested in all five conditions on five separate days. The order in which conditions were administered was counterbalanced between dingoes using a Latin square (Appendix 2, Table A2.2).

Procedure

The experimental procedure was identical for dog and dingo subjects. In all trials, the experimenter held up two pieces of food, called the subject and confederate partner by using the command "Come [subject/confederate partner name]!" The order in which names were called was counterbalanced within session. The experimenter then bent down and simultaneously placed a piece of food on each of two plates (or simultaneously touched the food to the plates in conditions where food was not being distributed), stood up, and signaled to the handlers that they could release the subject and partner. Subjects were then given approximately five seconds to approach (mean approach interval time for dogs: 4.37 ± 1.33 seconds (s), mean approach interval time for dingoes: 5.03 ± 1.81s). After the subject and confederate partner approached, the experimenter returned the subject to his/her handler and then returned the confederate to his/her handler. If a subject

did not approach on a given trial, the experimenter asked the handler to hold the leash and made a motion to return the dog in order to keep all movements during the experiment consistent regardless of subject behavior. Similarly, in conditions where the confederate partner was absent, the experimenter continued to pretend to return the absent confederate to the confederate handler (who was always present).

If a subject did not approach for five consecutive trials, the session was stopped to avoid causing unnecessary stress to the subjects. This never happened during the baseline half of sessions but happened regularly during the test half of sessions (28% of dog test sessions; 51% of dingo test sessions). In cases where a trial was deemed invalid during testing (e.g. due to a mistimed dog release by the handler) the trial was redone.

Food rewards for both dogs and dingoes consisted of small meat-flavored treats. The majority of dogs were given small pieces of sausage (Natural Balance™ Dog Food Roll, beef formula). In cases where a subject had a food allergy or refused to eat sausage on pre-test trials, they were tested using Zuke's™ Mini Naturals Dog Treats or the owner's treats. Dingoes were tested using small pieces of raw meat (either pieces of beef tip or a small dollop of minced meat). All food pieces were approximately the same size. Food rewards were present during all sessions, even during conditions where no food was distributed, to control for the possibility that the presence of high value food rewards could affect subjects' behavior.

Video coding and dependent variables

All sessions were recorded and research assistants coded data from video recordings. Videos were coded for several different measures. First, trials were inspected for

experimental error. To this end, coders ensured that on all trials dogs were paying attention to the food presentation, that the experimental presentations were done correctly and that subjects were released by their handlers using the correct method and at the correct time (see below for numbers and details regarding excluded trials).

Second, coders recorded subjects' approach behavior, specifically whether a subject approached the plate during a given trial. A subject was considered to have approached when he/she had two front paws in or on the approach box (see Fig. 4.1). Two measures were recorded from approach behavior: 1) absolute number of approaches during both the baseline half of the session and during the test half of the session, and, 2) the trial number of the subject's first non-approach ("first stop trial"). If a subject approached on all 15 trials, his/her first stop trial was recorded as being on "Trial 0" for the purpose of graphing and on "Trial 16" for the purposes of analyses. This was to ensure that the direction of differences between first stop trials on different conditions trials was accurate.

Third, coders recorded subjects' reaction time on each trial. Reaction time was coded as the duration of time between the moment the handler released the subject and the moment the subject first entered the approach box. Additionally, to ensure that trials were roughly the same duration, the entire trial interval was also coded (the time between the subject's release and the moment the experimenter turned to return the subject to the handler).

Finally, coders watched for two types of subject referencing behavior: references towards the experimenter ("subject-to-experimenter") and references towards the subject

handler ("subject-to-handler"). References were recorded as a binary present/absent variable and were recorded only if they occurred within the trial interval.

Each sessions was watched and analyzed by a research assistant. A random subset of the dogs' sessions (16 sessions, 11.1% of total, 482 trials) and dingo sessions (6 sessions, 10.9% of total, 177 trials) were independently re-coded for reliability. Reliability for categorical variables is reported here as percent agreement rather than as Cohen's kappa scores because for most of the variables there were fewer than 10 observations in a given category (e.g. experimenter error). With low frequency observations, percent agreement better represents reliability than Cohen's kappa (Nelson & Cicchetti, 1995; Shrout et al., 1987).

Reliability on all categorical variables was high (attention: dogs = 99.6%, dingoes = 98.3%; experimenter error: dogs = 99.8%, dingoes = 100%; handler error: dogs = 98.7%, dingoes = 98.9%; approach: dogs = 100%, dingoes = 98.3%; subject-to-experimenter references: dogs = 89.2%, dingoes = 89.8%, subject-to-handler references: dogs = 97.7%, dingoes = 91.0%). Reaction time was also coded reliably: coders times were highly correlated (dogs: Pearson's correlation, $r(383) = 0.98$, $P< 0.001$; dingoes: Pearson's correlation, $r(123) = 0.99$, $P<0.001$). The difference between coders' assessment of subjects' approach times was small (dogs: average difference = 0.02s; dingoes: average difference between coders = 0.36s).

After video coding, data were examined and processed by KM. During processing, trials that coders deemed invalid were excluded from the data set (dogs: 25 trials, 0.6% of total, 4 trials excluded due to lack of attention, 1 due to experimental error, 20 due to

handler error; dingoes: 14 trials, 0.9% of total, 11 trials excluded due to lack of attention, 1 due to experimenter error, 2 due to handler error).

Analyses

All statistical analyses were conducted with R statistical software (version 2.15.1, R Foundation for Statistical Computing, 2012). Approach and referencing behavior were analyzed using Generalized linear mixed models (GLMMs) with binary response terms. Total trial number differed slightly across sessions because some sessions were stopped after five consecutive non-approaches and due to the exclusion of invalid trials. To control for this, all GLMMs used raw data rather than proportional data.

Reaction time data were log transformed and analyzed using Linear Mixed Models (LMMs), as the transformed response term had a normal error distribution. All mixed models were run using R package lme4 (Bates et al., 2012). First stop data were analyzed using nonparametric tests.

In all mixed models subject identity (ID) was fit as a random effect to control for repeated measures. All analyses began with a null model, which included only ID as an explanatory variable to test how much variation in each dependent variable could be accounted for by individual variation. Following this, a full model was created, which included all predictors of interest. Full models were compared to null models using likelihood ratio tests (LRT) to understand whether including predictors provided a better fit to the data than simply including ID. A minimal model was then created from the full model by sequentially dropping terms in the model and testing whether their inclusion

improved the model. All figures show raw data and were created using ggplot2 (Wickham, 2009).

Ethical note

This work was approved by Harvard's Standing Committee on the Use of Animals in Research and Teaching (Protocol 28-25).

RESULTS

Species differences

Before investigating condition effects on dog and dingo behavior, I examined whether there were any overall differences between the species on approaches, reaction time and referencing (Fig. 4.2). Dogs were more likely to approach overall compared to dingoes (Fig. 4.2a; $X^2_1 = 9.38$, $P = 0.002$). Dogs also tended to approach faster than dingoes (Fig. 4.2b; $X^2_1 = 6.79$, $P = 0.009$). Finally, compared to dingoes, dogs showed higher levels of both subject-to-experimenter referencing (Fig. 4.2c; $X^2_1 = 20.92$, $P< 0.001$) and subject-to-handler referencing (Fig. 4.2d; $X^2_1 = 4.23$, $P = 0.04$). Taken together, these results demonstrate overall species differences in some of the variables of interest in this task, suggesting that dogs were more motivated to approach and referenced humans more than dingoes. Given these differences, all subsequent analyses are performed separately for dogs and dingoes in order to investigate the relative effects of experimental condition within each species.

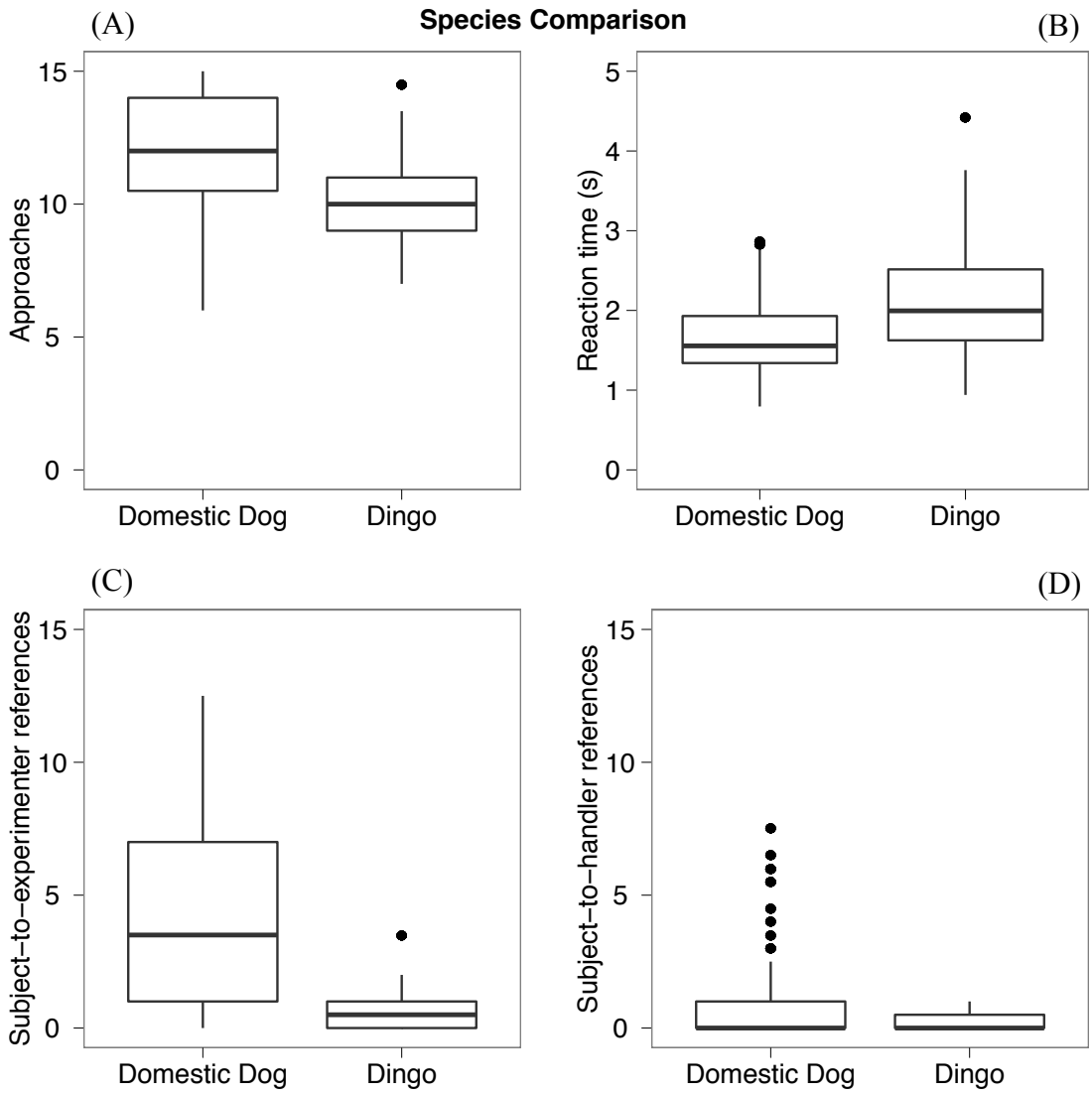

Figure 4.2. Boxplots generated from raw data showing number of approaches, reaction time (s) and referencing behavior for dogs and dingoes. Black lines bisecting each box show median values, boxes represent inter-quartile ranges, lines extending from boxes indicate minimum and maximum values and black circles indicate outliers.

Approaches and first stop

Dogs

To examine dogs' approaches in this task, the first analysis tested whether subjects were sensitive to the presence of a food reward. Did subjects approach less in the test half of sessions, when they were not being rewarded, compared to the baseline half of sessions, when they were being rewarded (Fig. 4.3a and 4.3c).

Dogs approached on 14.82 ± 0.52 trials in the baseline half of sessions while on the test half of sessions, dogs approached on 9.31 ± 4.23 trials. Session half (baseline vs. test) was a significant predictor of approach behavior (X^2_1= 1001.1, P< 0.001): subjects tended to approach more in the baseline half of sessions than in the test half of sessions. This shows that dogs were indeed sensitive to the presence of a reward and approached more when they were being rewarded for doing so. Approaches in the baseline did depend on session type (each dog was tested on the Inequity condition and a control, within subject measure) or on control group (each dog was assigned to one of four control groups, a between-subject measure). I ensured that there were no substantive differences between the dogs assigned to each control group by checking that there were no disparities in dogs' propensities to approach in the Inequity condition across the four different control groups. This finding validates the between-subject study design and allows inferences to be drawn from the group of 72 dogs as a whole.

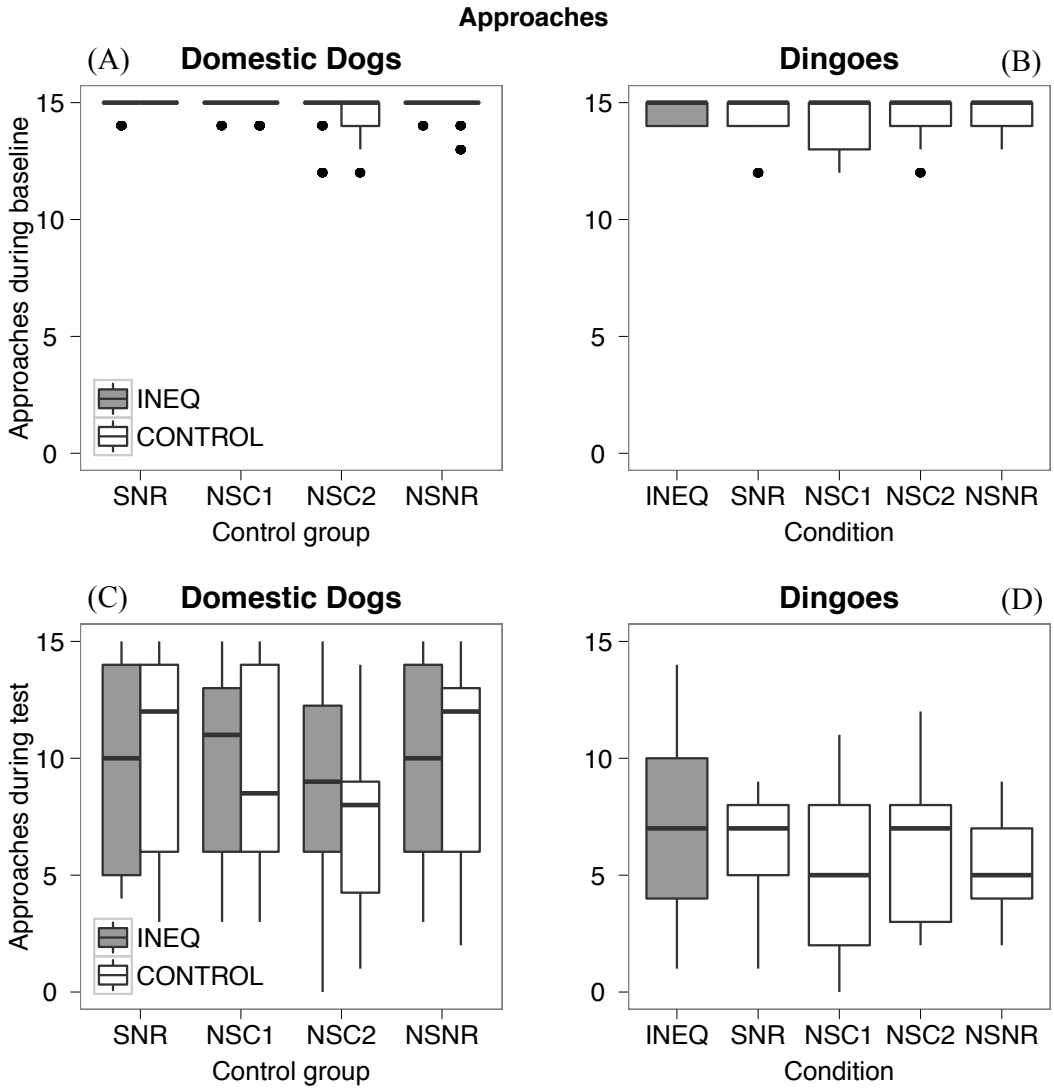

Figure 4.3. Boxplots generated from raw data showing number of approaches during baseline (top row; both subject and partner received a reward) and test sessions (bottom row) for dogs (N = 72) and dingoes (N = 11) across conditions. Boxes are shaded by test day: each dog was tested in the Inequity condition (INEQ) on one day and on one of four control conditions (CONTROL) on another day. All dingoes were tested in Inequity and each of the controls on five different days. On each day, subjects participated in both baseline and test sessions. Conditions were as follows: Inequity (INEQ), subject not rewarded while partner received a reward; Social Non Reinforced (SNR, N = 19 dogs), neither subject nor partner rewarded; Non-Social Control 1 (NSC1, N = 18 dogs), subject not rewarded and partner absent but reward delivered to partner's empty plate; Non-Social Control 2 (NSC2, N = 16 dogs), identical to First Non-Social Control but with a non-social baseline; Non-Social Non Reinforced (NSNR, N = 19 dogs), partner absent and no food distributed on plates. Black lines bisecting each box show median values, boxes represent inter-quartile ranges, lines extending from boxes indicate minimum and maximum values and black circles indicate outliers.

To test the hypothesis that dogs would be less likely to approach in the Inequity condition compared to the controls (Fig. 4.3c), a GLMM model was run on a subset of the approach data from the test half of sessions. In this model, approach was included as the binary response term and session type (Inequity vs. control), control group (Social Non Reinforced, First Nonsocial Control, Second Nonsocial Control or Nonsocial Non Reinforced) and order (dog tested in Inequity or control first) were included as predictor variables. Order was not a significant predictor and was dropped to create a minimal model (Appendix 2, Table A2.3). Results showed a significant interaction between control group and session type (X^2_3= 8.91, P = 0.031). As Fig. 4.3c shows, this effect is driven by the fact that dogs in the Second Non-Social Control group were less likely to approach in the control session (the completely non-social session) than the Inequity. A similar trend was seen in the other nonsocial control, First Non-Social Control (Fig. 4.3c). This finding indicates that there may have been social influences on dogs' approach behavior: dogs were less motivated to approach overall when tested in non-social conditions.

To test the hypothesis that dogs would stop approaching earlier in the Inequity condition than in the control conditions, I compared first stop trials across sessions (Fig. 4.4). I ran comparisons within each control group using Wilcoxin Rank Sum tests. None of the tests revealed a significant difference (Ps > 0.2). This result suggests that dogs did not cease participation in this task earlier in Inequity compared to the controls.

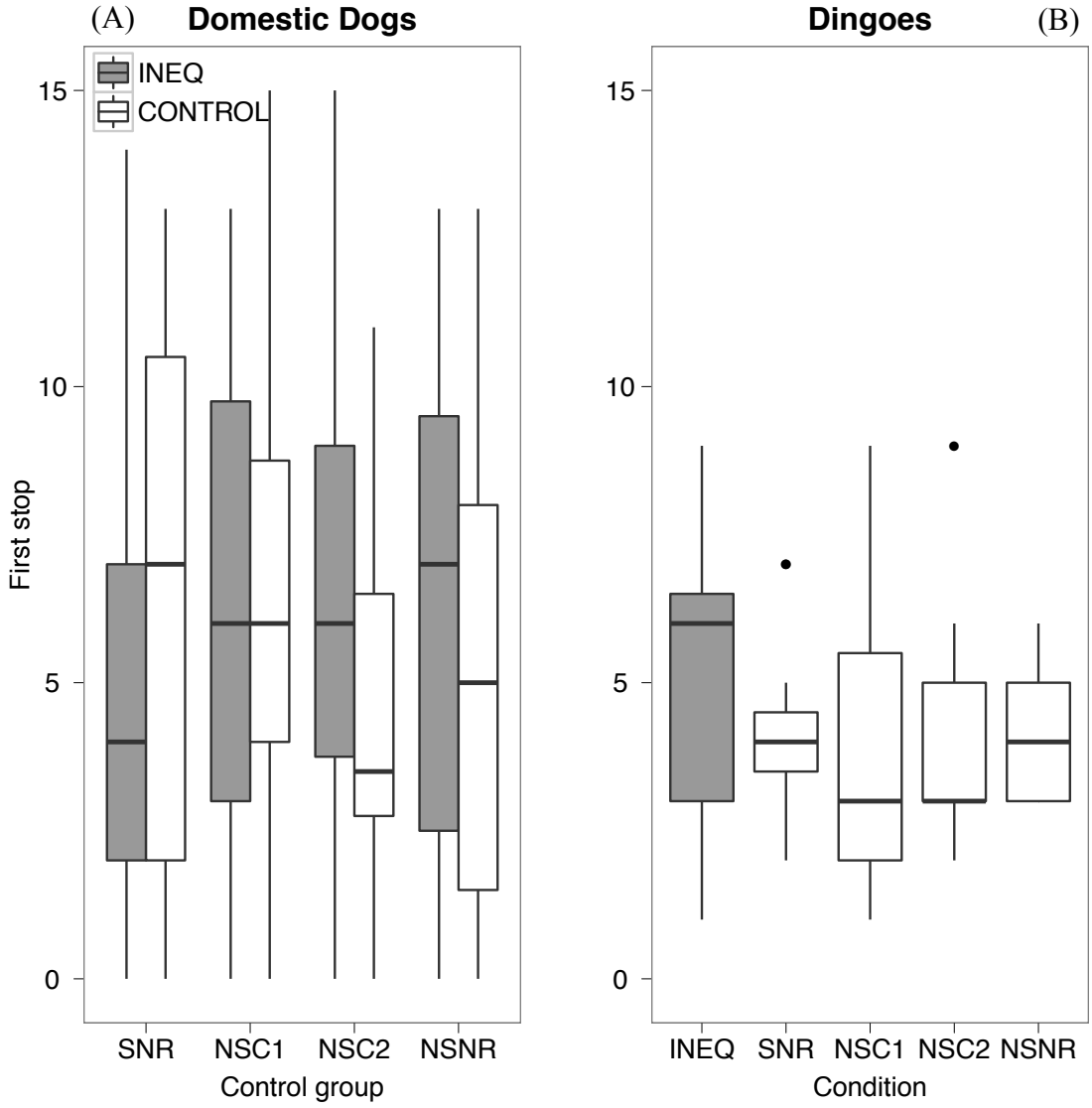

Figure 4.4. Boxplots generated from raw data showing the trial on which subjects first decided not to approach (first stop) during test sessions for dogs (N = 72) and dingoes (N = 11) across conditions. Boxes are shaded by test day: each dog was tested in the Inequity condition (INEQ) on one day and on one of four control conditions (CONTROL) on another day. All dingoes were tested in the Inequity condition and each of the controls on five different days. Conditions were as follows: Inequity (INEQ), subject not rewarded while partner received a reward; Social Non Reinforced (SNR, N = 19 dogs), neither subject nor partner rewarded; Non-Social Control 1 (NSC1, N = 18 dogs), subject not rewarded and partner absent but reward delivered to partner's empty plate; Non-Social Control 2 (NSC2, N = 16 dogs), identical to First Non-Social Control but with a non-social baseline; Non-Social Non Reinforced (NSNR, N = 19 dogs), partner absent and no food distributed on plates. Black lines bisecting each box show median values, boxes represent inter-quartile ranges, lines extending from boxes indicate minimum and maximum values and black circles indicate outliers.

Dingoes

To investigate whether dingoes approached less on Inequity compared to the controls, I followed the same method as above. I first asked whether dingoes approached more in the baseline half of sessions compared to the test half of sessions (Fig. 4.3b and 4.3d). As this figure shows, dingoes were more likely to approach in the baseline half of sessions than the test half of sessions. Thus, like dogs, dingoes were sensitive to the absence of food and were more likely to approach when they were being rewarded for doing so. Dingoes approached on 14.35 ± 0.96 of baseline trials. In the test half of sessions, on the other hand, they approached on 6.02 ± 3.13 trials. In a GLMM of dingo approach behavior, session half was a significant predictor of dingoes' approaches (X^2_1 = 505.53, P<0.001). There were no differences in baseline approaches across the five sessions (X^2_4 = 2.99, P = 0.559).

To test the hypothesis that dingoes were especially averse to the absence of food in the social inequity context, I ran a GLMM with approach behavior during test sessions as the response term and condition as the predictor variable. Condition was not a significant predictor of approach behavior (X^2_4 = 3.99, P = 0.408).

To investigate whether dingoes stopped earlier in some conditions than others (Fig. 4.4b), I ran a Friedman's ANOVA comparing first stop trials in the test half of session across conditions and there were no differences (X^2_4 = 3.90, P = 0.42). Together, these results suggest that dingoes' approach behavior was not affected by experimental condition but that dingo subjects consistently approached less in the absence of food than when they were being fed.

Reaction time

Dogs

Before investigating whether dogs approached more slowly in Inequity compared to the controls, I asked whether session half was a significant predictor of reaction time. Dogs approached faster on the baseline half of sessions (1.33 ± 0.43 s) than on the test half of sessions (1.97 ± 0.63 s). Indeed, session half was a significant predictor in a GLMM (X^2_1 = 1188.2, P<0.001). Given this difference between the session halves, subsequent analyses address each half separately.

I next examined whether dogs differed in their baseline reaction time across different sessions. In this model, there was a significant interaction between control group and session type (X^2_3 = 43.70, P< 0.001), which was driven by the fact that dogs tended to approach more slowly during the baseline half that preceded to the Second Non-Social Control – that is, during the one baseline condition without a partner.

Finally, I examined whether dogs differed in their reaction time in the experimental half of sessions across different conditions (Fig. 4.5a). To do this I ran a LMM with logged reaction time as the response term and control group, session type and order as predictors. The inclusion of these predictors did not improve the model fit relative to the null model, which included only subject ID as an explanatory term (X^2_5 = 1.77, P = 0.88). In sum, dogs were faster to approach when they were being rewarded for doing so but their reaction time did not depend on the context in which reward inequity was presented.

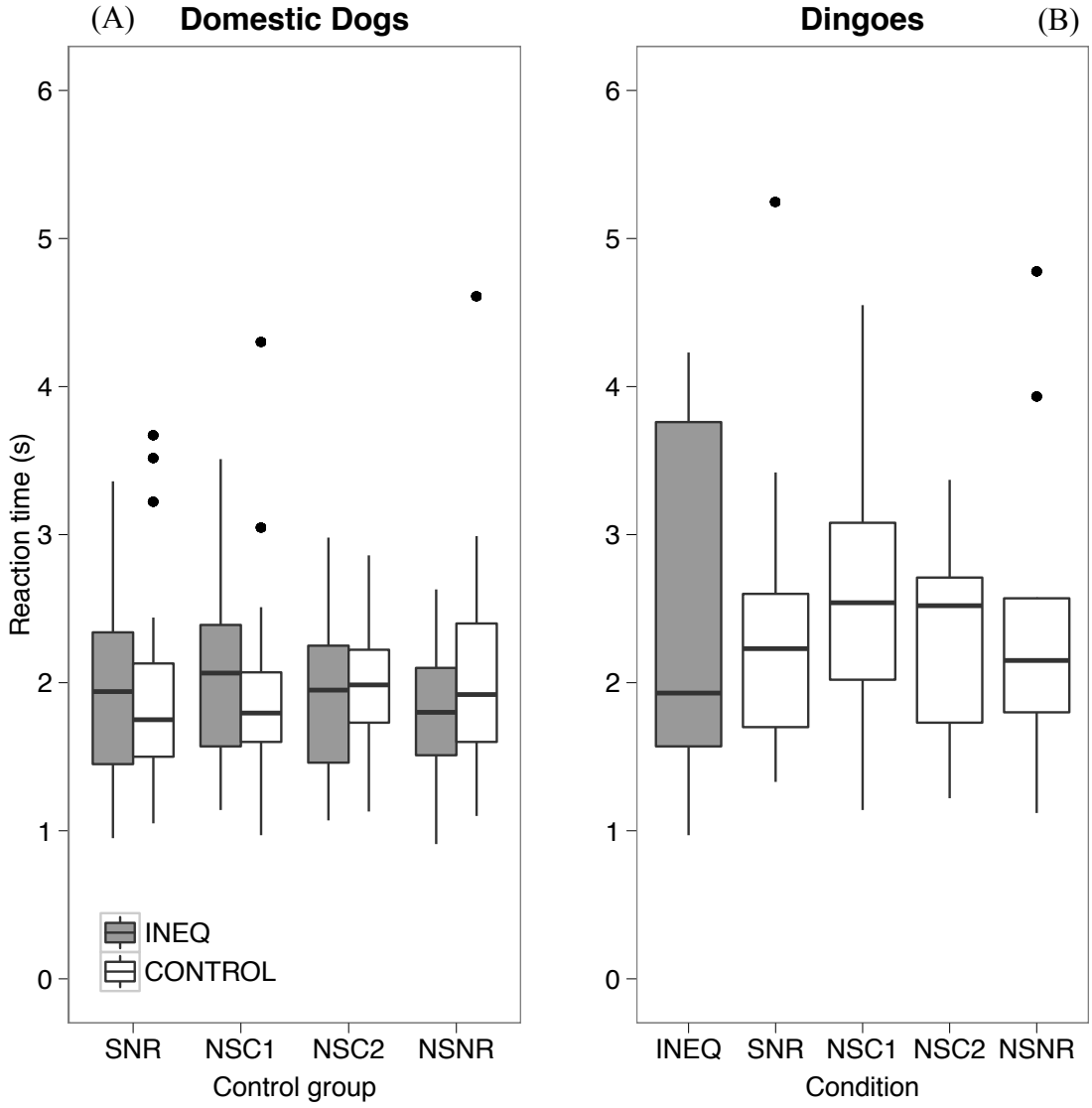

Figure 4.5. Boxplots generated from raw data showing reaction time - the time between subject release and approach - in seconds (s) during test sessions for dogs (N = 72) and dingoes (N = 11) across conditions. Boxes are shaded by test day: each dog was tested in the Inequity condition (INEQ) on one day and on one of four control conditions (CONTROL) on another day. All dingoes were tested in the Inequity condition and each of the controls on five different days. Conditions were as follows: Inequity (INEQ), subject not rewarded while partner received a reward; Social Non Reinforced (SNR, N = 19 dogs), neither subject nor partner rewarded; Non-Social Control 1 (NSC1, N = 18 dogs), subject not rewarded and partner absent but reward delivered to partner's empty plate; Non-Social Control 2 (NSC2, N = 16 dogs), identical to First Non-Social Control but with a non-social baseline; Non-Social Non Reinforced (NSNR, N = 19 dogs), partner absent and no food distributed on plates. Black lines bisecting each box show median values, boxes represent inter-quartile ranges, lines extending from boxes indicate minimum and maximum values and black circles indicate outliers.

Dingoes

To investigate reaction time in dingoes, I followed the same steps as outlined for dogs. Dingoes approached more quickly in the baseline half of sessions: the mean reaction time in the baseline half of sessions was 1.85 ± 0.68 s while in test half of sessions mean reaction time was 2.45 ± 0.96 s. In a LMM, session half was a significant predictor of logged reaction time (X^2_1 = 116.32; P <.001). Reaction time did not vary across baseline sessions (X^2_4 = -8.21, P = 1) nor did reaction time during the test half of sessions depend on experimental condition (Fig. 4.5b; X^2_4 = -12.87, P = 1). These results suggest that, like dogs, dingoes approached more quickly when they were being fed than when they were not being fed, but that unlike dogs their reaction time in the absence of food was independent of social context.

Human Referencing behavior

Dogs

Dogs looked more at the experimenter during the baseline half of sessions (5.72 ± 4.85 references) than during the test half of sessions (2.72 ± 3.16 references; X^2_1 = 227.62, P< 0.001). A further investigation of experimenter references during the baseline halves revealed a significant interaction between control group and session type (X^2_3 = 21.55, P< 0.001). This interaction was due to the fact that dogs in the Second Non-Social Control group were less likely to look at the experimenter during the baseline half preceding the control session (i.e. the baseline which did not include a partner) than the baseline preceding the Inequity session.

Similarly, an examination of subject-to-experimenter referencing in the test half of sessions (Fig. 4.6a), showed a significant interaction between control group and session type (X^2_3 = 17.02, P< 0.001), which appears to be driven by the fact that dogs tend to reference less in the Second Non-Social Control and First Non-Social Control conditions compared to the other conditions (Appendix 2, Table A2.4 for model output; minimal model excluded order because it was not significant). That is, dogs looked less at the experimenter during test sessions where the confederate dog was absent, indicating that there were social influences on dogs' referencing behavior towards the experimenter.

I next asked whether subjects differed in their propensity to look back at their handlers across the different experimental conditions (Fig. 4.6c). Dogs showed low levels of subject-to-handler referencing and these references did not vary by session half (baseline half = 0.9 ± 2.06 references; test half = 0.77 ± 1.37 references). A model investigating subject-to-handler referencing in relation to session half revealed that the addition of this term did not improve the model fit relative to the null model (X^2_1 = 0.13, P = 0.718). Thus, no subsequent analyses were performed. As Fig. 4.6c shows, subject-to-handler referencing behavior was a low frequency behavior in dogs, which most likely accounts for the lack of variation between baseline and test session halves.

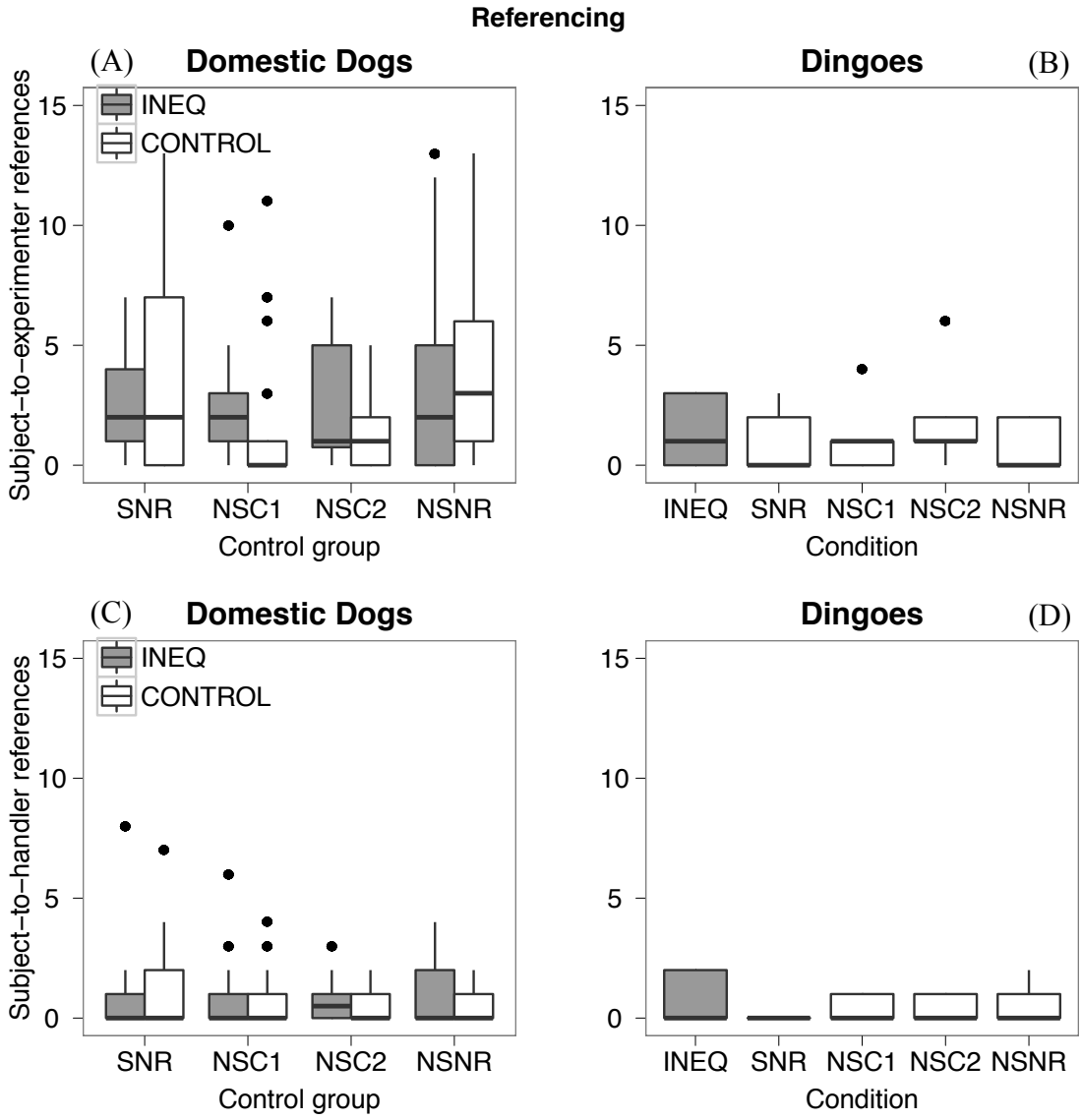

Figure 4.6. Boxplots generated from raw data showing number of subject-to-experimenter references (top row) and subject-to-handler references (bottom row) during test sessions for dogs ($N = 72$) and dingoes ($N = 11$) across conditions. Boxes are shaded by test day: each dog was tested in the Inequity condition (INEQ) on one day and on one of four control conditions (CONTROL) on another day. All dingoes were tested in the Inequity condition and each of the controls on five different days. Conditions were as follows: Inequity (INEQ), subject not rewarded while partner received a reward; Social Non Reinforced (SNR, $N = 19$ dogs), neither subject nor partner rewarded; Non-Social Control 1 (NSC1, $N = 18$ dogs)), subject not rewarded and partner absent but reward delivered to partner's empty plate; Non-Social Control 2 (NSC2, $N = 16$ dogs), identical to First Non-Social Control but with a non-social baseline; Non-Social Non Reinforced (NSNR, $N = 19$ dogs), partner absent and no food distributed on plates. Black lines bisecting each box show median values, boxes represent inter-quartile ranges, lines extending from boxes indicate minimum and maximum values and black circles indicate outliers.

Dingoes

I investigated referencing behavior in dingoes, using the same method as above. While the overall rate of subject-to-experimenter referencing was low, dingoes tended to look more at the experimenter during the experimental half of sessions (1.07 ± 1.25 references) compared to the baseline half of sessions (0.2 ± 0.4 references). Indeed, in a GLMM, session half was a significant predictor of subject-to-experimenter references (X^2_1 = 47.31, P< 0.001). This result is in the opposite direction to that observed for subject-to-experimenter references in dogs. Dingoes did not differ in their experimenter referencing behavior across experimental conditions (Fig. 4.6b; baseline half of sessions: X^2_4 = 4.37, P = 0.359; test half of sessions: X^2_4 = 5.39, P = 0.249).

Dingoes differed in their propensity to look at handlers between the baseline and experimental halves (X^2_1 = 24.32, P< 0.001). Again, the overall rate of referencing was low, but dingoes were more likely to look at their handler during the experimental sessions (0.35 ± 0.61 references) compared to baseline sessions (0.02 ± 0.13 references). There were no differences in their level of referencing across experimental conditions (Fig. 4.6d, baseline half of sessions: X^2_4 = 3.23, P = 0.52; test half of sessions: X^2_4 = 8.74, P = 0.068).

DISCUSSION

This study tested dogs and dingoes on an identical inequity aversion task in order to understand whether inequity aversion, which has previously been reported to occur in dogs (Range et al., 2009), is specific to dogs or is shared with another closely related social canid. The goal of this study was to distinguish between two hypotheses for the

expression of inequity aversion in dogs: 1) inequity aversion is the product of domestication (defined above); 2) inequity aversion is a product of the demands of intra-specific cooperation.

Surprisingly, neither dogs nor dingoes showed inequity aversion in this study. Both dogs and dingoes showed a higher level of motivation to approach in this study when they were being rewarded for doing so: both species approached more overall and more quickly in the baseline half of sessions, when both subject and partner were rewarded for approaching the plate, compared to the test half of sessions, where subjects were never rewarded. However, contrary to the prediction that subjects would be least motivated to approach in the inequity condition, neither dog nor dingoes were sensitive to the absence of a reward when their partner was getting rewarded compared to the four control conditions. Indeed, the only condition that stands out from the others is the completely non-social control (NSC2), which did not include the participation of a confederate partner. In this condition, dogs approached less and referenced the experimenter less than in the other conditions. A plausible explanation for this finding is that the presence of a social partner influenced dogs' motivation by making the task more salient. This could explain subjects' lower level of engagement in the absence of a partner.

A comparison of overall behavior between dog and dingo subjects revealed a number of difference between the two species: dogs approached more, approached more quickly and showed more social referencing compared to dingoes. These findings are consistent with other studies that found dogs to be motivated to interact with humans (Fonberg et al., 1981; McIntire & Colley, 1967; but see Feuerbache & Wynne, 2012).

Furthermore, the observed difference in human referencing behavior is consistent with work that has compared referencing between dogs and dingoes (Smith, 2010).

An examination of subject-to-experimenter referencing behavior in this task revealed an unexpected difference between dogs and dingoes: dogs referenced the experimenter relatively more when they were being rewarded than when they were not being rewarded whereas dingoes showed the opposite pattern. This was unexpected because past work found that dogs reference humans when they are unable to solve a problem (Miklósi, et al., 2003). It therefore seems surprising that dogs did not attempt to engage the human experimenter more in the conditions where food was not being put on the plate. It is possible that dogs in this task did not understand the human experimenter's role in the experiment or were not viewing the absence of food as a social problem. Alternatively, because subjects only had a short time to approach, they may have spent most of the test trial intervals searching for absent food, which would have decreased opportunities for human referencing.

Dingoes exhibited experimenter referencing in the same direction as found by past work (Miklósi, et al., 2003; Smith & Litchfield, 2010). However, given the lack of evidence for a clear pattern in dogs, it would be premature to say that their pattern of referencing is evidence that they were treating the absence of food as a social problem that required human intervention.

One potential issue concerns that fact that all subjects were run first in a baseline condition and then in a test condition. A benefit of this design is that each test session varied only one or two contextual elements (presence of a partner and presence of partner's food), allowing for clear comparisons across sessions. A problem with this

design, though, is that the presence and absence of food were conflated with order. That is, it is difficult to make a strong claim that the decrease in approaches in the test half of sessions relative to baseline was related exclusively to the absence of food. Rather, another potential cause for a decrease in approach behavior could be a decrease in motivation over the course of a session's trials. While this potential design flaw does not change the interpretation of this study's results, as it was designed for comparisons across conditions, it does mean that strong conclusions about how subjects react to the absence of food must be tempered.

The fact that dogs did not show inequity aversion in this study raises the question of why dogs in the Range et al. (2009; 2012) task did. One possibility is that Range et al. only tested familiar dogs whereas the present study only tested unfamiliar dogs. Some researchers have argued that the relationship between participants in inequity aversion tasks may have an important effect on individuals' tolerance of inequity (Brosnan et al., 2005; Horowitz, 2012; Range et al., 2012). While the present study was designed with the goal of controlling for the potential effects of relationship, it is worth exploring why familiar dogs may exhibit inequity aversion while unfamiliar dogs do not.

First, a relatively rich interpretation of the effect of relationship on inequity aversion would be that a stable relationship makes individuals more likely to attend to the relative distribution of payoffs and effort and thus more likely to respond to inequity when paired with a familiar partner. This interpretation suggests that all dogs have the capacity to identify and respond to inequity but dogs exhibit inequity aversion only in the context of a familiar pair. If this were true, it could explain why Range et al. (2009), who tested familiar dogs, found evidence for inequity aversion while my study did not.

However, this idea would weaken the claim that inequity aversion is integral to cooperation generally and, instead, suggest that it is a flexible trait that is only expressed under specific contexts.

A second possibility is that an individual might develop the ability to identify and respond to inequity only after they have been in a stable relationship. This explanation is fundamentally developmental and posits a simple associative account to explain why familiar dogs show inequity aversion while unfamiliar dogs do not. If two dogs live in a household with a human who routinely feeds them at the same time, it would be relatively easy for an individual to learn a simple rule of thumb: when my partner gets food from a human, I will most likely get food from a human. By this account, what looks like inequity aversion in familiar pairs, is really a reaction to a violation of this learned association. Future work could attempt to distinguish these two hypotheses by attempting to train the association of "equality" in one group while not training it in another group of dogs and then comparing both groups performance on an inequity task.

Another potential difference between the present study and those of Range et al. is that the current study used a task that is not habitually reinforced by humans (i.e. approach). I did this because I wanted to be able to test a range of breeds and two different species, which would not be feasible with the Range et al. design. It is possible that dogs would have responded more strongly to an unequal reward distribution between themselves and a partner had I arranged for them to perform a behavior for which they are typically rewarded. However, if this were true, then we would have good evidence that dogs only express inequity aversion when they have been trained to expect an equal payout for performing a behavior. In other words, we would have evidence that apparent

inequity aversion is the result of the violation of a trained association as opposed to a response to inequity per se.

Whatever the reason for between-study variation in the expression of IA by dogs, it is clear that dog inequity aversion is, at the very least, context-dependent or otherwise labile. Future work should seek to understand the contexts under which inequity aversion is expressed in dogs. More broadly, researchers may need to be more cautious when drawing conclusions about the evolved psychology of a species from one type of task.

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CHAPTER 5

SOCIAL INFLUENCES ON INEQUITY AVERSION IN CHILDREN

INTRODUCTION

The occurrence of extensive cooperation in human societies creates numerous opportunities for exploitation by free riders (Boyd & Richerson, 1992, 2005; Chudek & Henrich, 2011). In order to avoid being exploited, individuals must regulate their contributions to cooperative endeavors by attending to their payoffs relative to those of social partners. In line with this reasoning, human adults show a strong aversion to inequitable payoff distributions, i.e. they sacrifice personal gain in order to avoid inequity (Fehr & Schmidt, 1999). For example, in the ultimatum game, people often reject allocations of resources that place them at a disadvantage relative to a partner (i.e. disadvantageous inequity; DI), preferring nothing to a small relative reward (Güth et al., 1982). This behavior violates predominant rational choice models that predict that people should accept any non-zero offer of a desirable resource (Camerer, 2003). More surprisingly, in some situations adults also reject advantageous allocations in which they receive more than a peer (advantageous inequity; AI; Dawes et al., 2007; Fehr & Fischbacher, 2003; Fehr & Schmidt, 1999). Despite some variation, an aversion to unequal resource distributions has been established in a wide variety of cultural communities (Henrich et al., 2005; Henrich et al., 2010; Herrmann et al., 2008), demonstrating the apparent ubiquity of inequity aversion across human populations.

Research on children and nonhuman animals demonstrates that inequity aversion is not restricted to human adults. Studies of children show that inequity aversion is an

important feature of early social development and point to an intriguing asymmetry in the development of DI and AI aversion. Recent studies have found that children develop an aversion to DI at about 4 years of age (Blake & McAuliffe, 2011; Fehr et al., 2008; Moore, 2009; Thompson et al., 1997) but do not develop and aversion to AI until later, around 8 years of age (Blake & McAuliffe, 2011; Shaw & Olson, 2012). Studies of nonhuman animals have raised the question of whether inequity aversion is unique to humans and have demonstrated that some nonhuman animals are sensitive to DI resource distributions (Brosnan & de Waal, 2003; Brosnan et al., 2005; Neiworth et al., 2009; Range et al., 2009; van Wolkenten et al., 2007 but see Brauer et al., 2006; Dubreuil et al., 2006; Fontenot et al., 2007; Roma et al., 2006; Wynne, 2004). These studies suggest that an aversion to DI resource allocations may have deep evolutionary roots. As yet, however, no study has conclusively shown that nonhuman animals are averse to AI allocations (Brosnan et al., 2010). Together, results from studies of children and nonhuman animals suggest that separate evolutionary and developmental mechanisms underlie the two forms of inequity aversion.

Empirical demonstrations of inequity aversion across adults, children and nonhuman animals raise the question of how inequity aversion could have evolved, given that it motivates individuals to prefer nothing to something. Theories to explain the evolution and expression of inequity aversion can be broadly grouped under two hypotheses. First, the *Social Hypothesis* (Brosnan, 2006, 2011; Fehr & Schmidt, 1999) suggests that inequity aversion is specific to the social domain and evolved as a means of regulating contributions to, and payoffs from, cooperative interactions. According to this hypothesis an aversion to inequity allows individuals to ensure that they are not

contributing more or less to cooperative activities than fellow cooperators and, ultimately, protects individuals from being exploited and from exploiting others. Second, the *Nonsocial Hypothesis* suggests that IA is a result of domain-general mechanisms such as reference dependence and loss aversion that allows individuals to gauge their own payoffs relative to expected payoffs (Chen & Santos, 2006; Kahneman & Tversky, 1979; Tversky & Kahneman, 1981). According to the Nonsocial Hypothesis, inequity aversion may be *used in* social interactions but did not necessarily evolve *for* social interactions per se. Sensitivity to lower-than-expected payoffs may indeed be useful even in non-cooperative contexts. For example, an attention to how one's payoffs compare to available payoffs, including those of conspecifics, could confer a benefit in a foraging context where individuals can alter foraging strategies based on information about what payoffs can be expected in a given environment (Chen & Santos, 2006).

The Social and Nonsocial hypotheses generate different predictions. First, according to the Social Hypothesis, rejections of unequal offers in AI and DI should occur only when resources are divided between social partners. Furthermore, individuals should only reject unequal allocations when their rejections affect their partner's payoff and not when their partner's payoff is fixed relative to their own. According to the Nonsocial Hypothesis, rejections of unequal offers can occur even when there is no social partner. However, they should occur only in disadvantageous situations (i.e. small rewards will be less desirable when a larger possible reward is present for comparison) and not in advantageous situations where one's payoff is already better than other available payoffs.

Distinguishing these hypotheses is critical to determining why humans show inequity aversion. However, only one study has directly compared a social with a non-social condition in a human allocation game. Sanfey et al. (2003) found that rejections in the ultimatum game were higher when disadvantageous unequal offers were made by a human partner compared to a nonsocial condition where similar 'offers' were made by a computer. Notably, however, individuals also rejected many unequal offers made by the computer, even though no human partner would have received the better deal if the offer had been accepted. Thus, rejections of inequitable offers were stronger in a social context, suggesting that social influences play an important role in the expression of inequity aversion in human adults. However, results from Sanfey et al (2003) demonstrate that inequity aversion in human adults is not necessarily specific to situations where subjects are interacting with a partner.

In contrast to studies of human adults, studies of inequity aversion in nonhuman animals have carefully examined the degree to which inequity aversion is specific to the social domain. One frequently cited experiment provides a useful example that is representative of the majority of animal inequity aversion tasks. In the first study of inequity aversion in a nonhuman species, Brosnan and de Waal (2003) gave pairs of capuchin monkeys (*Cebus apella*) equal payoffs or unequal payoffs in return for trading a token. Results showed that subjects were least likely to trade a token when their partner received a high value reward for free while they had to trade a token for a low value food item. However, subjects also showed high refusals in a nonsocial condition, where high value food was placed in an adjacent cage and they were given the option to trade for a low value item. The fact that subjects continued to refuse trading opportunities in a

nonsocial condition showed that while inequity aversion may be mediated by social context, it was not specific to the social context. Furthermore, in this task, offers were produced by a third party (i.e. the experimenter) and rejections did not affect the social partner's payoff (Henrich, 2004). Given this, subjects may have used rejections to signal to the experimenter that they were not content with their payoffs.

As illustrated in the example above, Brosnan and de Waal's (2003) study and several similar nonhuman animal studies of inequity aversion have failed to provide strong support for the Social Hypothesis for two reasons. First, rejections of unequal offers are found regularly in nonsocial contexts (Brauer et al., 2006; Brosnan & de Waal, 2003; Brosnan, et al., 2005; Dubreuil, et al., 2006; Fontenot, et al., 2007; Neiworth et al., 2009). Second, animal tasks are typically designed such that recipients receive their payoffs regardless of the actors' decision (Brauer et al., 2006; Brosnan & de Waal, 2003; Brosnan, et al., 2005; Dubreuil, et al., 2006; Fontenot, et al., 2007; Henrich, 2004; Neiworth et al., 2009; Range et al., 2009; Roma et al., 2006; van Wolkenten, et al., 2007). Thus, it is unclear why deciders would reject unequal offers given that, unlike human studies of inequity aversion, rejections do not affect the overall payoff distribution. One possibility is that rejections are simply a means of signaling to the distributer (i.e. the experimenter) that subjects desire a better reward.

Despite the inconclusive nature of results from nonhuman animal studies, comparative research offers a critical methodological lesson for the study of inequity aversion in humans. Manipulations of the social context and of the role of the experimenter are essential for understanding the mechanisms that underlie rejections of personal gain in reaction to inequity. Indeed, manipulations of this kind are critical to

testing the Social and Nonsocial hypotheses for the evolution of inequity aversion. Furthermore, to understand whether social context differentially affects the expression of DI and AI aversion, it is important to investigate the role of social influences on inequity aversion in a situation where these two processes are separable. Accordingly, we studied the role of social influences in the development of DI and AI aversion in children, where AI and DI follow different development trajectories.

Our first study asks whether children reject unequal reward allocations in an effort to solicit more favorable allocations from the experimenter. According to the Social Hypothesis, children reject inequity in order to deprive a partner of advantageous or disadvantageous payoffs. This assumes that the main social interaction in the Inequity Game is between the decider and his or her partner. Alternatively, the main social interaction in the Inequity Game may be independent of the partner's presence and may instead be between the decider and the experimenter. In this scenario, rejections of unequal allocations may be a signal to the experimenter that the decider wants a better offer. If this is the case, deciders should reject unequal allocations more frequently when the experimenter deliberately generates inequitable divisions of resources compared to when inequality is randomly generated. On the other hand, if children's rejections are not intended as a signal to the experimenter, their frequency should not be affected by whether offers were made deliberately or randomly.

Our second study provides a direct test of the Social Hypothesis by testing children on an Inequity Game (Blake & McAuliffe, 2011) in the absence of a social partner. The Inequity Game is a face-to-face task in which children were partnered with an unfamiliar peer. One child (the decider) decides whether to accept or reject allocations

of candy. The decider's decisions determine both their own and their partner's payoff. If inequity aversion in children is a specifically social phenomenon, we expect few, if any, rejections in the nonsocial version of the game regardless of whether it involves AI or DI. However, if the Non-Social Hypothesis is true, children should continue to reject DI and AI offers in the same pattern as they did in the original, social version of the inequity game.

To understand whether social factors differentially influence DI and AI aversion, we tested children's responses to both forms of inequity.

GENERAL METHOD

Inequity Game

The method used in these studies closely follows that described in Blake and McAuliffe (2011). In the original Inequity Game two children sat face-to-face and were assigned one of two roles. One child (the "actor" or "decider") controlled a pair of handles, which were used to make decisions, while the other child (the "partner" or "recipient") sat across from the decider and could not reach the handles. The experimenter placed allocations of Skittles® on both sides of the apparatus (see Appendix 3, Fig. A3.1 for a photograph), always placing the candies on the recipient's side first in order to ensure that the decider paid attention to the recipient's payoff before perceiving their own.

Before starting the game the experimenter demonstrated how the handles work: the decider could accept the allocation by pulling the green handle which tilted the trays outwards, causing Skittles to fall into bowls on each side of the apparatus. The decider

could reject the allocation by pulling the red handle, which caused the trays to tip inwards, causing Skittles to fall into the middle bowl, where neither child was able to obtain them. Subjects were told that any Skittles that fell into their bowls could be taken home at the end of the game but that neither they nor their partner would take home the Skittles in the middle bowl. After the game was explained in this way, the subjects were given practice trials to ensure that they understood the apparatus including the effects of pulling both handles. The practice trials were as follows: 1-1 (1 for decider, one for recipient); 0-1 (DI; 0 for decider, 1 for recipient) and 1-0 (AI; 1 for decider, 0 for recipient). If a subject accepted all warm-up trials they were given an extra 1-1 trial and asked to try the red handle.

Analyses

All statistical analyses were conducted with R statistical software (version 2.15.2, R Foundation for Statistical Computing, 2012). Decision data were analyzed using Generalized Linear Mixed Models (GLMMs) with a binary response term (accept or reject; Bolker et al., 2009). Mixed models were run using the package 'lme4' (Bates et al., 2012). In all models subject identity (ID) was fit as a random effect to control for repeated measures.

Our GLMM procedure was as follows: (1) we examined a null model, which included subject ID as the only explanatory variable to test how much variation in the response term could be accounted for by individual variation; (2) we created a full model, which included predictor variables and all two-way interactions between Distribution (equal vs. unequal) and the other predictor variables (see Table 5.1 for a description of

predictor variables); (3) the full model was compared to the null model using a likelihood ratio test (LRT) to test whether the inclusion of predictors provided a better fit to the data than subject ID alone. Unless otherwise noted, full models provided a better fit to data than null models; (4) a minimal model was created from the full model by sequentially dropping single terms from the model and testing whether their inclusion improved the model fit using likelihood ratio tests.

Table 5.1. Description of predictor variables used in analyses of children's decisions to accept or reject reward allocations in Study 1 and Study 2.

Condition	Fixed effect with two levels: disadvantageous inequity (DI), advantageous inequity (AI)
Distribution	Fixed effect with two levels: equal (1-1), unequal (DI: 1-4 or AI: 4-1)
Age Group	Fixed effect with three levels: 4&5, 6&7, 8&9
Actor Gender	Fixed effect with two levels: male, female
Origin[1]	Fixed effect with two levels: deliberate, random
Order[1]	Fixed effect with two levels: deliberate block first, random block first
Order[2]	Fixed effect with two levels: equal block first, unequal block first

[1] Variable is unique to Study 1
[2] Variable is unique to Study 2

To examine whether children's decision varied over test trials, we used Wilcoxin signed-rank tests. All tests were two-tailed and alpha was set a 0.05. Figures show raw data and were created using the 'ggplot2' package (Wickham, 2009). Binomial confidence intervals were calculated using the Agresti-Coull method (Agresti & Coull, 1998).

STUDY 1: ARE CHILDREN SIGNALING TO THE EXPERIMENTER?

We tested whether children were more likely to accept unfair offers that were not under the experimenter's control compared to those that were under the experimenter's control. To this end, we performed the Inequity Game with a decider and a partner sitting face-to-face and we manipulated the origin of the offers such that half of the trial distributions were deliberately determined by the experimenter (hereafter, "deliberate" offers) while the other half of trial distributions were randomly determined by cards (hereafter, "random" offers) that had different distributions printed on them (see Appendix 3, Fig. A3.2 for an illustration of cards).

Methods

Participants

Children aged 4-9 were recruited in public parks in the Boston area (Blake and McAuliffe, 2011). Parents were approached and asked if their child would be interested in participating in a game where she/he gets to take home candy. If parents consented, children were escorted to a testing area containing the Inequity Game test apparatus. We tested a total of 124 pairs (decider age range 4;0-9;9, 59 female deciders). Participant information for Study 1 is reported in Appendix 3, Table A3.1.

Design

Children were assigned to one of two conditions: disadvantageous inequity (DI; N=64, 26 female deciders) or advantageous inequity (AI; N=60, 33 females). Offer origin

(deliberate or random) and distribution (equal or unequal) were tested within subjects, and inequity type (AI or DI) was a between-subject factor. This meant that each pair of children received three deliberate equal offers (1-1), three deliberate unequal offers (either DI, 1-4, or, AI, 4-1), three random equal offers (1-1) and three random unequal offers (either DI, 1-4, or, AI, 4-1). Offer origin was blocked so that pairs received six random offers followed by six deliberate offers or vice versa, with equal and unequal trials randomized within block.

Procedure

Before administering the randomly generated offers, the experimenter showed the subjects the cards and explained how they determined the distribution. The decider was then asked two questions to make sure she/he understood that the offers were not under the experimenter's control. First, the experimenter asked the child "*Do you know what the next card will be?*" and then "*Do I know what the next card will be*?" If a subject did not say "no" to these two questions, the experimenter stated that the distribution would be a surprise for everyone. The majority of children spontaneously answered these questions correctly. However, 24 children did not (17 children in DI; 7 children in AI; 19% of total sample). The pattern of our results was the same regardless of whether these children were included in analyses. If parents consented, we videotaped sessions (93% of sessions). Data were analyzed from video coding for these sessions (115 out of 124) and from live coding for the non-recorded sessions (9 sessions).

Results

Results from Study 1 are shown in Fig. 5.1a and 5.1b.

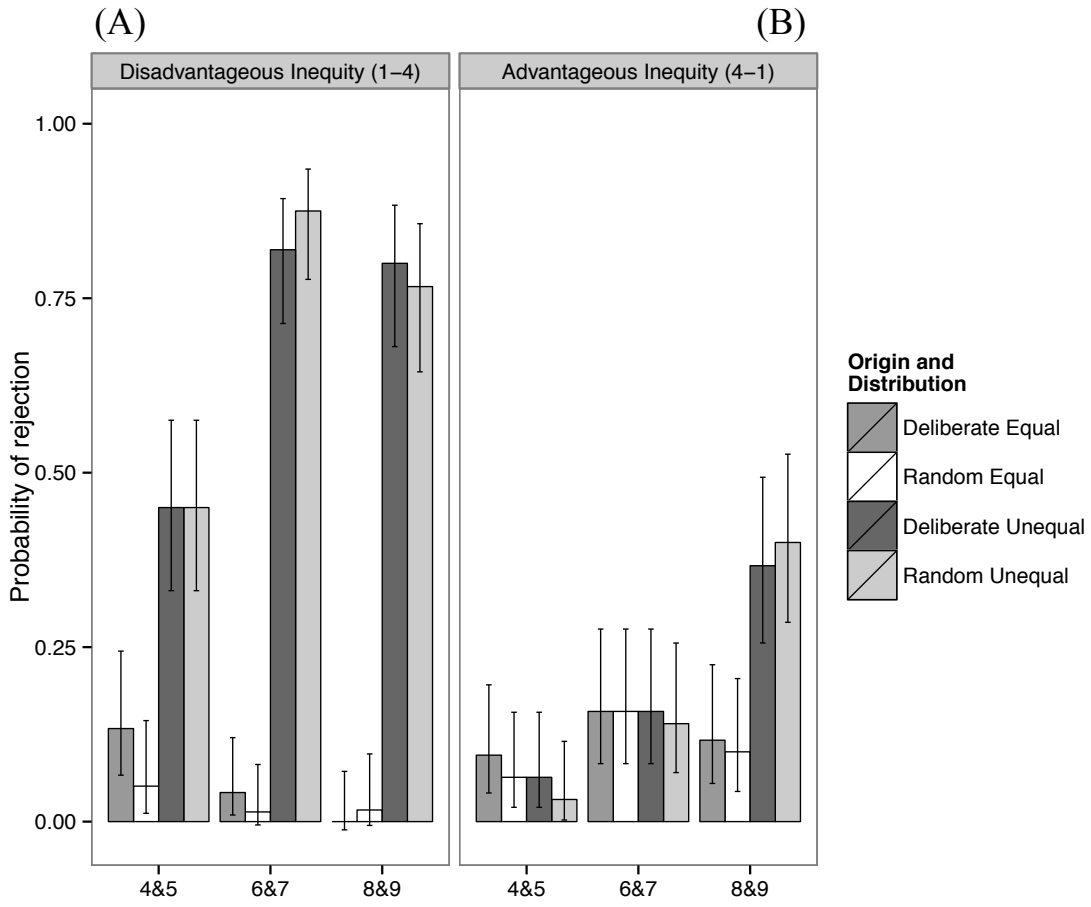

Figure 5.1. Probability of reward allocation rejection in Study 1, in which reward allocations were either generated deliberately by the experimenter or randomly generated by a deck of cards. Rejections are shown for the disadvantageous inequity (DI) condition (left) and the advantageous inequity (AI) condition (right). Subjects were assigned either to the DI condition (N = 64 pairs) or to the AI condition (N = 60 pairs). In the DI condition, subjects received one piece of candy while either one piece (equal distribution) or four pieces (unequal distribution) were placed on the recipient's side of the apparatus. In the AI condition, subjects received either one piece of candy (equal distribution) or four pieces (unequal distribution) while one piece was placed on the recipient's side of the apparatus. In both the DI and AI conditions, subjects received three of each trial type: 1) deliberate equal; 2) random equal; 3) deliberate unequal and 4) random unequal. Error bars represent 95% confidence intervals.

This figure illustrates that children responded differently to the two types of inequality, rejecting more offers in the DI condition than in the AI condition. In contrast, their rejections of equal offers were similar across both conditions. This observed interaction between Distribution (equal vs. unequal) and Condition (DI vs. AI) was a significant predictor of children's decisions in a GLMM of children's decisions (accept or reject) as a function of the following terms: Condition, Distribution, Origin, Age group, Actor gender, Order and the interaction between Distribution and Condition (LRT, $X^2_1 = 123.97$, $P < 0.001$). Because subjects' decisions about reward allocations differed between conditions, all subsequent analyses were conducted separately for DI and AI.

Results from the DI condition are shown in Fig. 5.1a. The main question motivating our analysis was whether children were more likely to reject disadvantageous unequal offers that were deliberately, as opposed to randomly, generated. As Fig. 5.1a shows, children did not distinguish between these two offer origins. A full GLMM of children's decisions in the DI condition showed that the interaction between Origin and Distribution was not significant (LRT, $X^2_1 = 2.45$, $P = 0.118$). We thus dropped this interaction from the model when creating the minimal model and additionally asked whether there was a main effect of Origin. This factor was not a significant predictor of children's decisions (LRT, $X^2_1 = 0.23$, $P = 0.635$). Given that the social origin of DI allocations did not affect children's decisions, we eliminated both the Origin and Order (deliberate or random block first) terms from our model.

Our minimal model (see Appendix 3, Table A3.2 for model output) showed that there were two significant predictors of subjects' decisions in the DI condition: (1) an interaction between Distribution and Age group (LRT, $X^2_2 = 35.19$, $P < 0.001$) and (2) an

interaction between Distribution and Actor Gender (LRT, $X^2_1 = 5.61$, $P = 0.018$). Fig. 5.1a clearly illustrates the interaction between Distribution and Age group: older children were more likely to reject unequal allocations than younger children but rejections of equal offers did not vary with age. The interaction between Actor Gender and Distribution was due to the fact that males were slightly more likely to reject equal offers and slightly less likely to reject unequal offers than girls in the DI condition (see Appendix 3, Fig. A3.3 for a depiction of this interaction).

We examined subjects' decisions in the AI condition following the same steps as outlined above. Results from the AI condition are shown in Fig. 5.1b. This figure illustrates that children did not distinguish between deliberately generated allocations and randomly generated allocations. Indeed, GLMMs revealed that neither the interaction between Origin and Distribution nor the main effect of Origin were significant predictors of subject's decisions in the AI condition ($X^2_1 = 0.09$, $P = 0.766$, $X^2_1 = 0.22$, $P = 0.638$, respectively).

Results from our minimal model showed that the only significant predictor of subjects' decisions in the AI condition was the interaction between Distribution and Age Group (LRT, $X^2_2 = 20.77$, $P < 0.001$; model output is shown in Appendix 3, Table A3.2). This interaction is illustrated by Fig. 5.1b: children across the three age groups were unlikely to reject equal offers and 4&5- and 6&7-year-olds rarely rejected advantageously unequal offers. Thus, children in the 4&5- and 6&7-year-old age group did not distinguish between equal and unequal offers in the AI condition. However, subjects in the 8&9-year-old age group tended to reject more unequal reward allocations than equal allocations. The finding that there is an interaction between Age group and

Distribution provides an important replication of the age trend in AI rejections reported in Blake & McAuliffe (2011).

In addition to examining overall rejections of equal and unequal allocations across DI and AI conditions, we asked whether subjects' tendencies to reject allocations varied across trials. Children received six equal trials and six unequal trials. We thus wondered whether repeated exposure to unequal reward allocations might increase their probability of rejecting such offers. To test this we used Wilcoxin signed-rank tests to compare children's decisions on their first three unequal trials to decisions on their last three unequal trials. To control for the possibility that children may simply reject more or less over time, we performed the same comparisons on equal trials. We performed these comparisons by condition and by age group (see Appendix 3, Fig. A3.4 for a graph showing decisions over trails). None of these comparisons revealed a significant difference between the first and last three trials (all Ps > 0.25). Thus, children's decisions did not vary over repeated trials.

Discussion

We found that children's levels of rejections did not differ between unequal offers that were deliberately generated by the experimenter and offers that were randomly generated by cards. Regardless of offer origin, 4- to 9-year-old children were likely to reject DI allocations and unlikely to reject AI allocations. This suggests that children did not reject DI offers in order to signal to the experimenter that he or she should distribute resources differently. Similarly, 8-9-year-olds children rejected more AI allocations than equal allocations, irrespective of whether the experimenter had control over offers. Indeed, AI

rejections in this study were particularly striking because they occurred even when the experimenter apparently had no control over the initial distribution. This result provides an important replication of Blake and McAuliffe (2011), demonstrating that AI rejections emerge relatively late in development, at 8-9 years of age.

It is possible that children may not have understood the card manipulation and instead assumed that the experimenter was in control regardless of how allocations were determined. We do not think this is the case given that the majority of children (81%) answered our card comprehension questions correctly, confirming that understood that the experimenter did not know what the next allocation would be. Furthermore, previous work suggests that children in the age groups that we tested are capable of distinguishing intentional from accidental outcomes and have a basic understanding of randomness (Tomasello et al., 2005; Xu & Denison, 2009). Instead, we argue that children in this study understood the card manipulation but did not use this understanding to guide their behavior in the Inequity Game. This result is consistent with similar work in children that shows that in a version of the UG, older children (7- to 10-year-olds) do not distinguish between intentional and unintentional unequal offers (Sutter, 2007).

The finding that children do not use rejections to signal to the experimenter is consistent with the idea that the main social interaction in the Inequity Game is between the actor and the recipient as opposed to between the actor and the experimenter. This finding is also consistent with the idea that children reject reward allocations in order to deprive their partner of either a more desirable (DI) or less desirable (AI) reward. However, an alternative explanation for rejections in the Inequity Game is that children are opposed to the unequal reward allocations themselves. In other words, it is possible

that children would reject unequal allocations regardless of whether or not they were paired with a social partner. To address this alternative explanation for rejections of inequity, we conducted a nonsocial version of the Inequity Game in which children were faced with unequal outcomes in the absence of a social partner.

STUDY 2: DO CHILDREN REJECT INEQUITY IN A NONSOCIAL GAME?

The goal of this study was to test whether children's rejections of unequal allocations in the Inequity Game are specific to situations where deciders were paired with a social partner. To this end, we conducted the Inequity Game with a decider but no recipient. We reasoned that if children reject allocations due to an aversion to the unequal outcomes themselves, then rates of rejection in Study 2 should be indistinguishable from those observed in Study 1. However, if children are importantly influenced by the presence of a social partner, we should expect to see a difference in rates of rejections between the two studies.

Method

Participants and design

We tested total of 201 children (107 females). As in Study 1, children were assigned to one of two conditions: disadvantageous inequity (DI; N = 98, 55 females; age range: 4;0-9;9; and advantageous inequity (AI), N = 103, 52 females; age range: 4;0-9;8. Participant information for Study 2 is reported in Appendix 3, Table A3.1.

Children were given 3 warm-up trials and 12 test trials. Children participated in either the DI condition or the AI condition (between subject). In both conditions, the test trials were blocked so that children received a block of 6 equal trials (1-1, 1 for decider, 1 on the other tray) and a block of 6 unequal trials (DI: 1 for decider, 4 on other tray; AI: 4 for decider, 1 on the other tray). Block order was counterbalanced across subjects.

Procedure

Children were recruited in public parks, as described in Study 1. The instructions were the same as above except that, here, the experimenter said that the Skittles on the other side of the apparatus would go back into the bag at the end of the game. To test their understanding of this, children were asked where the Skittles on the other side of the apparatus would go at the end of the game. If children failed to spontaneously answer this question correctly (15 children; 7 children in DI and 8 in AI; 7.5% of total sample), the experimenter would restate that the Skittles went back in the bag at the end of the game. Excluding children who did not answer this question correctly did not change the pattern of our results.

Video recordings were available for 98.5% of subjects and unavailable for three subjects for whom we did not have video consent. Data were analyzed from video coding for all but these sessions. Data from live coding were analyzed for the three non-recorded sessions.

Results

Nonsocial Game

Results from Study 2 are shown in Fig. 5.2a and 5.2b.

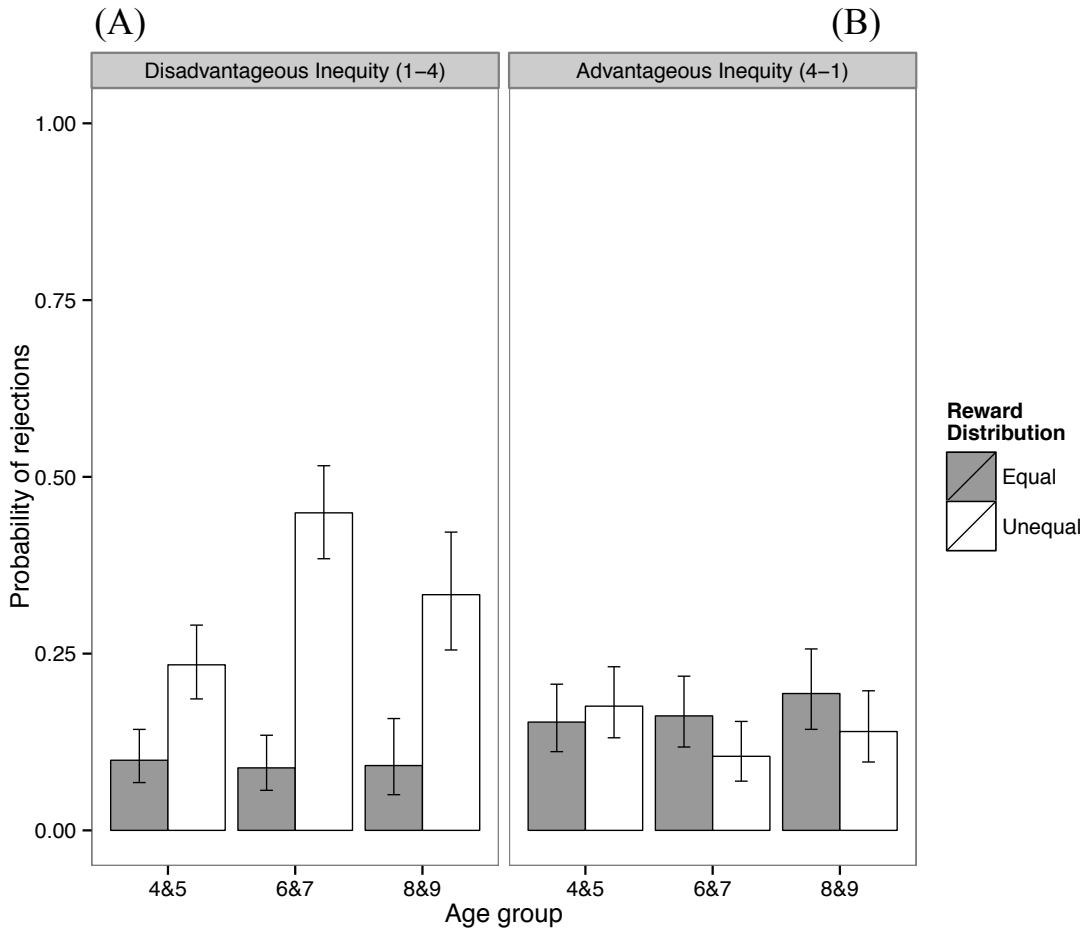

Figure 5.2. Probability of reward allocation rejection in Study 2, the nonsocial version of the inequity game. Rejections are shown for the disadvantageous inequity (DI) condition (left) and the advantageous inequity (AI) condition (right). Subjects were assigned either to the DI condition (N = 98) or to the AI condition (N = 103). In the DI condition, subjects received one piece of candy while either one piece (equal distribution) or four pieces (unequal distribution) were placed on the other side of the apparatus. In the AI condition, subjects received either one piece of candy (equal distribution) or four pieces (unequal distribution) while one piece was placed on the other side of the apparatus. In both the DI and AI conditions, subjects received six equal and six unequal trials. Error bars represent 95% confidence intervals.

Children responded differently to the two types of inequality, rejecting more offers in the DI condition than in the AI condition while their rejections of equal offers were similar

across both conditions. As in Study 1, we found that the interaction between Condition and Distribution was a significant predictor of children's decisions (LRT, $X^2_1 = 74.91$, $P < 0.001$). Consequently, all subsequent analyses were conducted separately for DI and AI.

Fig. 5.2a illustrates children's probability of rejecting unequal compared to equal offers in the DI condition. Examination of this figure suggests that children in all age groups rejected more unequal offers (1-4) than equal offers (1-1). Furthermore, this figure indicates that older children were more likely to reject unequal offers than younger children. In contrast, rejections of equal offers were stable across age groups. Indeed, our minimal model confirmed that interaction between Age Group and Distribution was a significant predictor of children's decisions in the DI condition (LRT, $X^2_2 = 10.03$, $P = 0.007$; see Appendix 3, Table A3.3 for model output).

To further explore the interaction between age and distribution, we examined the proportion of children in each age group that rejected more unequal offers than equal offers using Chi square tests. In 4&5-year-old and 8&9-year-old children this proportion did not differ from chance (4&5-year-olds, 20 out of 42 children; X^2 (1, $N = 42$) = 0.095, $P = 0.75$; 8&9-year-olds, 13 out of 20 children; X^2 (1, $N = 20$) = 1.8, $P = 0.18$). In children ages 6&7, on the other hand, the proportion of children that rejected more unequal than equal trials did differ from chance (6&7-year-olds, 24 out of 36 children; X^2 (1, $N = 36$) = 4.00, $P = 0.045$). This suggests that 6&7-year-olds were especially likely to reject more disadvantageously unequal than equal reward allocations.

Results for the AI condition are shown in Fig. 5.2b. As this figure illustrates, children rarely rejected unequal offers that benefited them more (4-1). Indeed, neither Age Group nor Distribution predicted rejections in our game. Our GLMM analyses

showed that a full model, including all predictors and two-way interactions with Distribution, provided only a marginally better fit to subjects' decision data than a null model that included subject ID as the sole explanatory term (X^2_9 = 16.51, P = 0.057). This finding suggests that inter-individual variation accounted for almost as much variation in subject behavior as did predictor variables and subject ID combined.

Our minimal model showed that the only significant predictor of children's behavior was the order in which blocks of trials were presented (LRT, X^2_1 = 7.50, P = 0.006; see Appendix 3, Table A3.3 for model output). This order effect was due to the fact that children who received the 4-1 block first rejected more trials overall (mean rejections overall = 1.2, mean rejections of 1-1 = 1.4, mean rejections of 4-1 = 1.0) compared to children who received the 1-1 block first (mean rejections overall = .65, mean rejections of 1-1 = .66, mean rejections of 4-1 = .64).

As in Study 1, we were interested in whether children's decisions varied across trials. To test this, we performed Wilcoxin signed-rank tests on subjects' first three unequal trials compared to their last three unequal trials. We also examined whether subjects' decisions about equal trials varied across trials using these same comparisons. Separate Wilcoxin signed-rank tests were performed for each age group within each condition (see Appendix 3, Fig. A3.5 for a graph showing decisions over trials). In two cases, we found a significant difference between the first and second three unequal trials. Children in the 6&7-year-old age group were less likely to reject disadvantageously unequal trials in the second group of three trials compared to the first group of three trials (W = 833, P = 0.030). Similarly, children in the 8&9-year-old age group were less likely to reject disadvantageously unequal allocations in later trials (W = 269.5, P = 0.049).

None of the other comparisons showed a significant difference between the first three and second three trials (*P*s > 0.2).

Study 1 and Study 2 compared

To examine whether children rejected fewer DI and AI offers in the nonsocial version of the game (i.e. when they were paired with a partner) than the social game, we compared results from Studies 1 and 2. Our main question was whether children were more likely to reject unequal offers in the social version of the task or whether rejections would be similar across social and nonsocial contexts. Figure 5.3a-d illustrates children's probability of rejection in the social and nonsocial versions of the Inequity Game. Children's rejections are shown separately by condition and distribution to reflect our method of analysis.

To address the question of whether rejections varied by social context (i.e. Study 1 or Study 2), we conducted four separate GLMMs that each tested whether subjects' decisions were predicted by an interaction between Experiment (social, i.e. Study 1 or sonsocial, i.e. Study 2) and Age Group. Results from these models showed that children's rejections of equal offers did not depend on social context (see Appendix 3, Table A3.4 for model output). The interaction between Age group and Experiment was not significant for either the DI or AI condition (DI: $X^2_2 = 4.05$, $P = 0.132$; AI: $X^2_2 = 1.14$, $P = 0.566$).

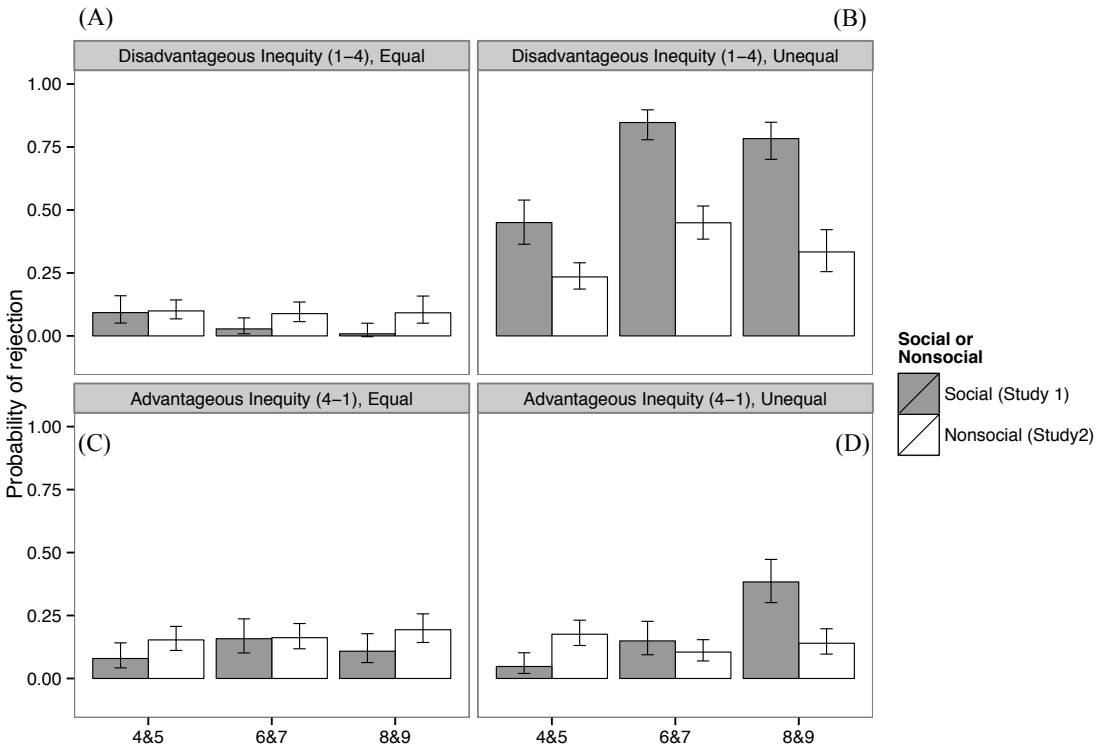

Figure 5.3. A comparison of the probability of rejecting offer allocations in Studies 1 (social) and 2 (nonsocial). Rejections are shown for the disadvantageous inequity (DI) condition (top row) and the advantageous inequity (AI) condition (bottom row). Within condition, rejections are show by equal distribution (1-1, left column) and unequal distribution (1-4 of 4-1, right column). Subjects were assigned either to the DI condition or to the AI condition. Within condition, subjects received six equal trials and six unequal trials. Error bars represent 95% confidence intervals.

In contrast, children's decisions about unequal reward allocations did vary by experiment. The interaction between Age group and Experiment was a significant predictor of children's decision in both the DI and AI conditions (DI: $X^2_2 = 30.03$, $P < 0.001$; AI: $X^2_2 = 7.26$, $P = 0.027$). Figure 5.3b and d illustrate these interactions. In the DI condition, children in all age groups rejected unequal offers more often in the social than the nonsocial version of the Inequity Game. In the AI condition, 8&9-year-old children rejected unequal offers (4-1) more often in the social game than in the nonsocial game.

However, 4&5- and 6&-7-year-olds' rejections of unequal reward allocations in the AI condition did not differ between social and nonsocial contexts.

Discussion

There are three main findings from Study 2. First, 4- to 9-year-old children tended to reject DI offers in a nonsocial situation. To our knowledge, this is the first study to demonstrate that children will reject inequity in a nonsocial version of a reward distribution game. Second, 4-9-year-old children tended to reject disadvantageous inequity more when they were playing with a social partner than when they were playing the nonsocial game. Third, whereas younger children accepted AI offers in both the nonsocial and the social versions of the game, 8 and 9-year-old children rejected advantageous offers, but only when they were paired with a social partner.

The fact that children in a nonsocial game often rejected DI offers suggests that their rejections in the social version of this game were not motivated purely by an aversion to having a smaller payoff than a social partner. Rather, in both nonsocial and social contexts children may have rejected DI offers in part because their payoff was relatively less than other potential payoffs. Rejections of DI offers in a nonsocial context are thus consistent with the Nonsocial Hypothesis that inequity aversion is built on a simple heuristic for gauging the relative value of one's payoff compared to an expected payoff (Chen & Santos, 2006; Kahneman & Tversky, 1979; Tversky & Kahneman, 1981; Santos & Lakshminarayanan, 2008). In the DI condition, children may have been comparing their allocations of skittles to other available allocations (i.e. they are comparing their single skittle to the possible allocation of four skittles) regardless of

whether another individual was benefiting from the differential payoff distribution. However, this reference-dependence explanation cannot fully account for children's rejections in the social game because rejections were significantly higher there than in the nonsocial version of the game.

Social partners are particularly important when children are faced with an AI allocation. Results from the AI condition show that children only rejected advantageous offers when playing the social version of the task: they accepted AI offers in the nonsocial task. This finding is consistent with the theory that DI and AI aversion follow different developmental pathways, and hence may be underpinned by different mechanisms.

GENERAL DISCUSSION

Combined, these two studies provide a detailed picture of how social influences affect children's decisions about unequal payoffs. Study 2 shows that social partners influence how children react to inequity, although their importance varies depending on the form of inequity. An aversion to advantageous inequity is clearly a specifically social phenomenon; 8&9-year-old children only rejected advantageous inequity when a partner was present. Disadvantageous inequity aversion, on the other hand, has an important nonsocial component; children at all ages rejected some DI allocations in the absence of a social partner. Importantly, however, DI aversion is influenced by social context; children rejected more DI offers in the social game than in the nonsocial game.

In Study 1, the experimenter's intentional delivery of unequal offers had no effect on children's decisions, suggesting that the main social interaction in the task is between

decider and recipient rather than between the decider and experimenter. Moreover, this demonstrates that rejections in the Inequity Game are not a signal to the experimenter, but are based instead on the relative rewards at stake. Additionally, Study 1 provides an independent replication of the age-shift reported in Blake and McAuliffe (2011) with 8 and 9-year-old children rejecting AI offers when playing the Inequity Game with a social partner.

Is inequity aversion specifically social?

The finding that an aversion to AI, but not DI, distributions is specific to situations where resources are distributed amongst social partners provides support for the idea that these two forms of inequity aversion show an asymmetry in their development and are underpinned by different cognitive processes (Blake & McAuliffe, 2011; Shaw & Olson, 2012). Moreover, this result is consistent with a theory that an aversion to AI resource distributions evolved *for* social interactions and is not based on domain-general mechanisms. However, the fact that AI aversion is specifically social in children cannot, by itself, help us distinguish between the Social and Nonsocial hypotheses because both hypotheses predicted that children would accept AI resource allocations in the nonsocial task.

Results from the DI conditions in these two studies, on the other hand, bear on the Social and Nonsocial hypotheses in important ways. In Study 2, 4- to 9-year-old children rejected DI offers at significant levels even when no peer would receive the larger reward. The fact that children in the nonsocial game would rather have nothing than accept a relatively small reward suggests that DI aversion in children has an important nonsocial

component. This result is surprising in light of work on adults where it is generally assumed that inequity aversion is a specifically social phenomenon and thus nonsocial tests are not typically conducted (see Sanfey, et al., 2003 for an exception).

Although there are clearly important social influences on DI aversion in children, DI aversion does not appear to be triggered exclusively by interactions with a social partner. Rather, our results suggest that unlike AI aversion, DI aversion may be built on a simpler domain-general process like reference-dependence (Chen & Santos, 2006; Kahneman & Tversky, 1979; Tversky & Kahneman, 1981), which is consistent with the Nonsocial Hypothesis for the evolution of inequity aversion. Future work is necessary to understand the specific mechanisms that underpin rejections of DI allocations in a nonsocial task but, minimally, we can conclude from our results that it may be necessary to revise the commonly held view that individuals only reject disadvantageous allocations in order to influence a partner's payoff. More broadly, we argue that a productive area for future work would be to understand why AI aversion is specifically social while DI aversion is not and to develop a theory for the evolution of inequity aversion that can account for this important dissociation by integrating the Social and Nonsocial hypotheses. Such an approach will also be instrumental in creating ties between studies of inequity across human adults, children and nonhuman animals.

Rejections of unequal allocations in the nonsocial game represent an intriguing similarity with nonhuman animal work where individuals commonly reject inequitable offers in nonsocial controls (Brauer et al., 2006; Brosnan & de Waal, 2003; Brosnan, et al., 2005; Dubreuil, et al., 2006; Fontenot, et al., 2007; Neiworth et al., 2009). While results from Study 2 cannot speak directly to the evolutionary origin of inequity aversion

in humans, they suggest at least two plausible explanations. First, it is possible that inequity aversion is indeed a purely social phenomenon in humans and rejections in the absence of a social partner are a misapplication of this aversion. In line with this hypothesis, children in our sample may have acquired an expectation about equity in the social domain and have erroneously applied this expectation to the nonsocial task. Alternatively, inequity aversion in humans may be built on domain-general mechanisms that are shared with nonhuman species (Kahneman & Tversky, 1979) and that is enhanced by social context. In line with this view, children perceive their payoff of 1 Skittle as less desirable when it is distributed alongside of a payoff of 4 Skittles compared to when it is alongside of a payoff of 1 Skittle. Children may react aversively to this payoff asymmetry regardless of whether it is benefiting a peer but their reactions to inequity are strongest when a peer benefits from the asymmetry. At present, we are unable to distinguish between these alternatives but view them as fruitful areas for future inquiry.

Are rejections a signal to the experimenter?

Study 1 was designed to test whether the critical social interaction in the Inequity game is between decider and experimenter or between decider and recipient. We tested this by asking whether children were rejecting unequal offers in the Inequity Game in order to signal to the experimenter that they were not happy with the payoff distribution. Results from this study show that deciders did not distinguish between unequal offers that were deliberately versus randomly generated by the experimenter, suggesting that children were most likely not attempting to signal to the experimenter with rejections. Further

evidence in support of the idea that children did not reject unequal offers in order to signal to the experimenter comes from the finding that there was a difference in levels of rejections in the nonsocial and social versions of the Inequity Game. If children's rejections in the game were solely motivated by a desire to signal to the experimenter, we would not expect to see this difference. Given these two lines of reasoning, we argue that the relevant social interaction in the Inequity game is between decider and recipient and that children show high levels of rejection in the social version of the Inequity Game because they are attempting to influence their social partner's payoff through rejections.

More broadly, the results from Study 1 have important methodological implications because they demonstrate that children's behavior in the Inequity Game is not driven by their interactions with an experimenter. Given that almost all studies of inequity aversion in children are done in the presence of an experimenter, this suggests that their behavior in these tasks is likely to be a product of their interaction with a peer as opposed to with the adult running the experiment.

Conclusion

Results from these studies provide insights into the ontogeny of inequity aversion in children. Social influences are undoubtedly important in the expression of inequity aversion in children and this is especially true for advantageous inequity aversion. However, there are also important nonsocial factors at play, as was evidenced by children's rejections of disadvantageous allocations in the nonsocial game. Thus, our results begin to paint a more nuanced picture of the emergence of inequity aversion in children. Understanding the social factors that influence the expression of inequity

aversion is critical to understanding its evolution and development but, to date, few studies have tested these influences empirically. Examining the social factors that influence inequity aversion in children and adults will help unite human inequity aversion studies with inequity aversion studies in nonhuman animals and will help shed light on the evolutionary and developmental processes that shape inequity aversion in humans.

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CHAPTER 6

LOOK WHO'S WATCHING: REPUTATION EFFECTS ON FAIRNESS IN CHILDREN

INTRODUCTION

Theoretical and empirical work has demonstrated how building a good reputation can be beneficial for cooperation. For example, adults who are viewed as cooperative are more likely to be the future recipients of cooperation themselves (Bolton et al., 2005; Boyd & Richerson, 1989; Leimar & Hammerstein, 2001; Milinski et al., 2002; Nowak, 2006; Nowak & Sigmund, 2005; Panchanathan & Boyd, 2003; Wedekind & Braithwaite, 2002; Wedekind & Milinski, 2000). Adults who are known cooperators are more likely to be the future recipients of cooperation (e.g. Wedekind & Milinski, 2000). Not surprisingly therefore, individuals tend to manage their reputations so as to be viewed as friendly, honest, and especially, cooperative (Goffman, 1959; Leary, 1996; Schlenker, 1980; Tedeschi, 1981).

Given the benefits of a good reputation, individuals are incentivized to provide others with an honest signal indicating that they are good cooperators (Barclay, 2010). One such signal is to show an aversion to advantageous inequality, where an individual has more than a peer (Dawes et al., 2007; Fehr & Schmidt, 1999; Loewenstein et al., 1989). An individual who is willing to incur a personal cost to prevent an advantageous

outcome demonstrates that they are willing to adhere to norms of fairness, even when such adherence is costly. Such costly signaling could ultimately benefit the signaler through direct or indirect reciprocation as well as through gains in status (Smith et al., 2005).

In this paper we seek to distinguish between two alternative explanations for the expression of advantageous inequity aversion. The first is that advantageous inequity aversion represents the internalization of a strong norm of fairness and, as such, is not influenced by reputational concerns. The alternative is that advantageous inequity aversion is motivated by a desire to build a reputation for fairness and, as such, is importantly influenced by who is watching.

Here we evaluate the relative importance of these two mechanisms by investigating reputational effects on advantageous inequity aversion in children. A previous study with US urban children suggest that advantageous inequity emerges late during the development, at around the age of eight years (Blake & McAuliffe, 2011). One plausible reason for the late emergence of advantageous inequity aversion is the onset of reputational concerns. Children may be rejecting advantageous allocations in order to signal to others that they are fair people. Indeed, by this age, children are able and motivated to strategically manage their reputations (Banerjee, 2002a; 2002b; Watling & Banerjee, 2007). Because reputational concerns are known to be in place at the time of the emergence of advantageous inequity aversion, we hypothesize that the expression of advantageous inequity aversion in children is dependent on audience effects. According to this hypothesis children are expected to reject advantageous allocations only when others are watching. Before describing our study, we first review a past study on

advantageous inequity aversion in children and, second, provide a brief overview of the relevant background on reputation and fairness in children and adults.

As children grow they increasingly take norms of fairness into account. This is especially clear in tasks where children must allocate resources between themselves and a peer (Benenson et al., 2007; Blake & Rand, 2009; Fehr et al., 2008; Moore, 2009; Olson & Spelke, 2008; Shaw & Olson, 2012). An important component of children's growing adherence to fairness norms is an aversion to inequitable resource distributions, which children express even when doing so comes at a cost to themselves (Blake & McAuliffe, 2011). Using an Inequity Game, Blake & McAuliffe's (2011) demonstrated that from four years of age, children from a US population in Boston rejected disadvantageous inequity, where the subject received less candy than a peer. Thus four-year-olds are able to assess their own potential payoff relative to their partner's potential gains and reacted accordingly. However it was not until around eight years of age that children began to reject advantageous inequity, where the subject received more candy than a peer. Eight-year-olds took longer to make decisions when faced with an advantageously unequal allocation of candy compared to equal allocations of candy, suggesting that instead of automatically rejecting inequitable offers, children experienced an internal conflict about whether to accept or reject the inequitable allocation.

There were two key aspects of the Blake & McAuliffe (2011) Inequity Game that may have importantly influenced children's decisions about advantageous inequity. First, the game was played face-to-face, meaning that children were asked to make decisions in front of a novel peer. Second, the game was played in public and thus children were making decisions about inequity in front of an audience, which typically included the

subjects' parents. Given the public nature of the game, it is unclear whether children were motivated either by an intrinsic desire for fairness or by a desire to appear fair in front of an audience.

It is plausible that older children sacrifice personal gain to avoid advantageous inequity in order to accrue reputational benefits since fair behavior in adults is clearly influenced by reputational concerns. For example, in studies of the dictator game, where one player is given the chance to offer any amount of a fixed amount of money to another player, adults are more generous when their identity will be made known to a recipient compared to when they can play anonymously (reviewed in Andreoni & Bernheim, 2009). Furthermore, adults will pay a cost to ensure that recipients are not aware that a dictator game is being played, allowing them to abscond without donating any portion of their endowment (Dana et al., 2006). These results suggest that by adulthood individuals are sensitive to the information that others can acquire about their generosity and suggest that they are motivated to appear fair in front of an audience. By the age of eight, children may understand the benefits of behaving fairly in front of an audience. Thus, the emergence of advantageous inequity aversion in older children may represent the onset of a more sophisticated ability to manage one's reputation for fairness as opposed to the internalization of a strong norm of fairness.

Indeed, as children age, their ability to present themselves appropriately to different audiences (i.e. their self-presentation ability) improves, suggesting a growing desire to meet others' expectations of how they should behave (Banerjee, 2002; Watling & Banerjee, 2007). Studies that ask children to articulate their reasons for changing the way they present themselves to different audiences have identified middle childhood (6-

11-years) as the age at which self-presentational abilities develop (Aloise-Young, 1993; Banerjee, 2002a; 2002b; Banerjee et al., 2010). However, the building blocks of more sophisticated self-presentational abilities appear at younger ages.

Sensitivity to audience is one such building block that is expressed by even younger children. Repacholi et al. (2008) showed that 18-month-olds attended to an experimenter's emotional reactions when interacting with different objects and used the memory of the experimenter's emotions to guide their own interactions with different objects: subjects avoided objects that had previously elicited anger in an experimenter. Critically, however, children only showed this avoidance when the experimenter could see them, indicating that they were able to regulate their behavior based on whether or not they were being watched (Repacholi et al., 2008). Hence, from a young age children are able to use audience cues to guide their behavior. However, these studies do not tell us whether children are able to change their behavior in front of an audience in order to manage their reputations.

Sensitivity to audience is a particularly interesting component of a child's social cognition because it plays a critical role in the development of several aspects of social behavior. One such aspect is rule following and, by extension, disobedience or cheating. Bucciol and Piovesan (2011; Shaw et al., in press) showed that the absence of an audience promoted cheating in 5-15-year-olds. In their study, subjects readily cheated on a coin-flipping task, where certain outcomes were rewarded, when no one was watching. Additionally, in a study on 6-11-year-old children, the presence of an audience deterred cheating on a task that required children to resist a selfish impulse (Houser et al., 2012). In 5-9-year-olds, the presence of an audience was shown to deter cheating even when the

audience was fabricated (Piazza et al., 2011). While these studies provided evidence that the presence of an audience influences the probability of cheating in children, they did not identify the age at which sensitivity to the presence of an audience influences others aspects of children's cooperative behavior, such as prosocial behavior.

Recent studies suggest that audience effects matter for cooperative behaviors broadly construed. Engelmann and colleagues (2012) showed that the presence of a peer onlooker not only deterred cheating in 5-year-olds, but also encouraged sharing, though the sharing effect was not statistically significant. In the Engelmann et al. task, children were able to steal or donate a sticker to an absent partner, and subjects were less likely to steal and more likely to donate when being observed by a peer. Similarly, Leimgruber et al. (2012) showed that 5-year-old children were more likely to be generous when they were being watched and when the onlooker was aware of the extent of their generosity. When they were their decisions could not be tracked by an onlooker, subjects revealed selfish tendencies. Similarly, Shaw et al. (in press) found that 6- to 8-year-old children opted for fair (equal) resource distributions when an experimenter was aware of their actions. However, fewer children opted for fair distributions when they could benefit from inequality without appearing unfair to the experimenter. Thus, by the age of five children's cooperative behavior appears to be influenced by reputational concerns

Together, results from studies examining children's sensitivity to their audience indicate that from a relatively young age children understand how others expect them to behave and are importantly influenced by the presence of observers. Moreover, these results point to reputation concerns that are important in guiding aspects of children's cooperative behavior, such as cheating, sharing and generosity. It is reasonable to

hypothesize, therefore, that reputational concerns are sufficiently important to 8-year-old children that they are willing to sacrifice personal gain when faced with advantageous unfairness. If this is true, children should show higher levels of advantageous inequity aversion when being watched by an audience compared to when in private. If advantageous inequity aversion is immune to audience effects, however, it is likely that its emergence represents the adoption of a strong norm of fairness rather than a costly reputational signal.

Here we directly test the hypothesis that reputational concerns have an important influence on fairness in children by asking whether Boston children ages 6-9 will reject advantageous inequity when under different conditions of privacy. Based on previous work (Blake & McAuliffe, 2011), we expected to see an increase in rejections of advantageously unequal offers between the younger (6-7-year-olds) and older (8-9-year-olds) age groups. Note that we expected to see this age shift in children sampled from the Boston population but do not assume that this same pattern of development is common to all populations (Henrich et al., 2005).

Our study is the first to explicitly address how the costly adherence to fairness norms and reputation concerns interact during development. We address this by focusing on children's rejections of advantageous inequity aversion because rejections of this form of inequity cannot be explained by a motivation to maximize one's own payoff relative to a peer. Specifically, we used a face-to-face Inequity Game in with 6-9-year-old children were partnered with an unfamiliar peer. We designed three different treatments that differed in the degree to which others could view subjects' allocation of candy relative to their partner. In the Public treatment, subjects received advantageous allocations of candy

in full view of both their partner and an audience of parents and adult onlookers. In the Recipient Ignorant treatment, subjects received advantageous allocations of candy without their partner knowing the distribution but in view of an audience. In the Private treatment, subjects received advantageous allocations of candy in private where they were hidden from both their partner and the audience.

We hypothesized that older children would show greater sensitivity to who is watching than younger children. Specifically, our study was designed to distinguish the relative merits of three hypotheses: 1) reputational concerns about fairness are in place in the 6-7-year-olds; 2) reputational concerns about fairness emerge in 8-9-year-olds; 3) reputational concerns about fairness do not emerge until after the age of 9. Distinguishing between these hypotheses will shed light on the question of whether rejections of advantageous inequity aversion are driven by reputational concerns or an internalized fairness norm.

In addition to examining levels of rejections of advantageous allocations, we tested the hypothesis that children would take longer to make decisions about advantageously unequal offers when in public compared to when in private. This finding would indicate that children were conflicted not just about inequity but also about others' expectations of their decision. An examination of children's reaction times provides a powerful means of looking beyond individual decisions and into the processes that underpin them (Blake & McAuliffe, 2011; Piovesan and Wengström, 2009; Rand et al., 2012).

METHOD

Participants

Subjects aged 6-9 were recruited in public parks in the Boston area. A total of 212 deciders (see below for description of decider role; 424 children in total) were tested. Deciders were separated into two age groups: 6-7-year-olds (N = 102, mean: 81.6 months, age range: 72-95 months) and 8-9-year-olds (N = 110, mean: 106.8, age range: 96-119 months) with approximately equal numbers of male and female deciders (see Appendix 4, Table A4.1 for a detailed sample breakdown). Deciders were tested in one of three conditions: Public (N = 72 pairs, mean: 94.15, age range: 72-118), Recipient Ignorant (N = 74 pairs, mean: 95.07, age range: 72-119) and Private (N = 66 pairs, mean: 94.82, age range: 71-119). Nine additional pairs participated in at least part of the task but were excluded from the final sample (6 excluded due to parental interference, 2 due to experimenter error, 1 due to a child getting upset).

Design

Children were randomly assigned to one of three treatments. In the *Public treatment* (Fig. 6.1a), a clear barrier was erected between the subjects such that both the audience and the recipient could see both players' payoffs. In the *Recipient Ignorant treatment* (Fig. 6.1b), an opaque barrier was erected between the subjects so that the recipient could not see decider's payoff but the audience could see the distribution on both sides of the apparatus. In the *Private treatment* (Fig. 6.1c), an opaque box was erected so that neither the recipient nor the audience could see the decider's payoff.

(a) Public (b) Recipient Ignorant (c) Private

Figure 6.1. Photographs of the Inequity Game apparatus with the barriers used in each of three treatments: (a) Public; (b) Recipient Ignorant; (c) Private. Deciders had access to the two handles and could pull the green handle to accept reward allocations, delivering candy to the two red bowls, or could pull the red handle to reject reward allocations, delivering candy to the center metallic bowl. In each of the three experimental treatments, a different barrier was erected which varied the amount of information available to the recipient and the audience.

Children were given 3 warm-up trials (see below) and 12 test trials. Following past work (Blake & McAuliffe, 2011), test trials were blocked so that children received a block of 6 equal trials (1-1, 1 for decider, 1 for recipient) and a block of 6 advantageous unequal trials (4 for decider, 1 for recipient). Block order was counterbalanced between subjects, within age groups and within decider gender. Each session, including training, lasted approximately 10-15 minutes.

Procedure

Pre-test procedure

Parents were approached by one of our team who asked if their child would be interested in participating in a game where he/she gets to take home candy. If parents consented and children assented, children were escorted to a testing area containing the Inequity Game test apparatus (Figure 6.1). In this task children were paired with an unfamiliar peer of approximately the same age. The two sat face-to-face and were randomly assigned to one of two roles. One child (the "decider") controlled a pair of handles, which were used to make decisions, while the other child (the "partner" or "recipient") sat across from the decider and could not reach the handles.

Introduction to barriers

Before starting the experiment, the experimenter introduced subjects to one of three barriers that would be used in the game. The barrier was erected on the apparatus and subjects were asked to inspect the apparatus from both sides of the barrier to ensure that they understood what could and could not be viewed from each player's perspective.

Explanation of apparatus

After this demonstration, the barrier was taken down and subjects were shown how the handles work: the decider could accept an allocation of candy by pulling the green handle which tilted the trays outwards, causing candies to fall into bowls on each side of the apparatus. In this case, children were asked to move any candies that fell into their bowls into paper bags so that subjects could not track the accumulation of candy by the other player. The decider could reject an allocation by pulling the red handle, tipping the trays inwards, causing candies to fall into the middle bowl, where neither child was able to obtain them. All bowls were padded with pieces of cotton so that the number of candies in each bowl could not be assessed by attention to auditory cues. Subjects were told that any candies that fell into their bowls could be taken home at the end of the game but that neither they nor their partner would take home the candies in the middle bowl.

Testing procedure

Small, colorful fruit-flavored candies (Skittles®) were used as food rewards in this experiment. When distributing rewards, the experimenter always placed candies on the recipient's side first in order to ensure that the decider paid attention to the recipient's allocation before attending to their own.

After explaining the apparatus, subjects performed practice trials to confirm that they understood how to use both handles. The practice trials were as follows: 1-1 (1 for decider, one for recipient); 0-1 (0 for decider, 1 for recipient) and 1-0 (1 for decider, 0 for recipient). Subjects who accepted all allocations in the warm-up trials were given an extra

1-1 trial and asked to try the red handle. After each decision, the experimenter stated the payoff distribution. For example, after a 1-1 trial, she would say to actor and recipient sequentially: "you can put your candy in your bag, and you can put your candy in your bag."

Following practice trials, and before test trials, subjects were once again shown one of the three barriers. When distributing rewards, the experimenter placed one candy on the recipient's side, erected a barrier and then placed one candy on the decider's side. To test subjects' understanding of the barriers, both deciders and recipients were asked whether they knew how much candy was on the other side of the apparatus. If deciders did not spontaneously confirm their understanding of this (7 children; 3.3% of total sample), the experimenter would clearly state what each player knew about the other's payoff.

Recipients would occasionally attempt to peak around the barrier, but their efforts were immediately thwarted by the experimenter. Participants rarely interacted after the experiment and few recipients asked about the actor's payoff post-game.

Coding

The main dependent measure was subjects' decisions to accept or reject reward allocations. These were coded from video recordings for 94% of subjects and from live coding for 12 subjects (6% of subjects), for whom we did not have video consent. All video data were double checked against live coded data by KM for consistency. Reliability between live coding and video coding was excellent: there were 8

disagreements in total (0.3% of trials) and all disagreements were found to be errors in entry from videos rather than from live coding. We are therefore confident that the live coded data for the 12 subjects that were not videotaped accurately represents their decisions.

In addition, we measured subjects' reaction time in the task: i.e., the time it took children to decide which handle to pull in each trial. Using Interact version 9, a child's reaction time was coded from the moment the experimenter finished distributing skittles and signaled to the child (by removing a stick that lay atop the trays) that he/she was free to pull a handle. Reaction time ended at the moment the child began pulling one of the handles. Two research assistants coded a random subset of 29 sessions (14% of total sample) for reliability. Their reaction time coding was highly correlated, $r(350) = 0.86$, $P < 0.001$, and the difference between their coded reaction time values was small (M = .04 seconds), and not significantly different from zero, paired t-test, $t(351) = -0.53$, $P > 0.50$.

Analyses

All statistical analyses were conducted with R statistical software (version 2.15.1, R Foundation for Statistical Computing, 2012). Decision data were analyzed using Generalized Linear Mixed Models (GLMMs) with a binary response term (accept or reject). Reaction time data were log transformed and analyzed using Linear Mixed Models (LMMs), as the transformed response term had a normal error distribution. All mixed models were run using R package lme4 (Bates et al., 2012).

In all models subject identity (ID) was fit as a random effect to control for repeated measures. In both decision analyses and reaction time analyses, we first examined a null model, which included ID as the only explanatory variable to test how much variation in the response term could be accounted for by individual variation. Following this, we created a full model, which included all predictors and interactions of interest (see Table 6.1 for a description of predictor variables).

Table 6.1. Description of predictor variables used in analyses of children's decision and reaction time data.

Decision	Distribution	Fixed effect with two levels: equal (1-1), unequal (4-1)
	Treatment	Fixed effect with three levels: Public, Recipient Ignorant, Private
	Age Group	Fixed effect with two levels: 6&7, 8&9
	Actor Gender	Fixed effect with two levels: male, female
	Recipient Gender	Fixed effect with two levels: male, female
	Order	Fixed effect with two levels: equal block first, unequal block first
Log latency	Distribution	as above
	Decision	Fixed effect with two levels: accept, reject
	Treatment	as above
	Age group	as above
	Actor Gender	as above
	Recipient Gender	as above

The full model was compared to the null model using a likelihood ratio test (LRT) to assess whether including predictors provided a better fit to the data than just ID. In all analyses the full model provided a significantly better fit to the data than the null model. A minimal model was then created from the full model by sequentially dropping terms in the model and testing whether their inclusion improved the model using likelihood ratio tests. Figures were created using raw data and, where appropriate, binomial confidence intervals were calculated using the Agresti-Coull method (Agresti & Coull, 1998).

RESULTS

Rejections of unequal offers: does age matter?

As figure 6.2 shows, on average, 8-9-year-old children were more likely to reject unequal offers than 6-7-year-old children, regardless of treatment. To test this statistically, we asked whether older and younger children differentially responded to the reward allocations. Indeed, there was a significant interaction between age and distribution (X^2_1 = 22.13, $P < 0.001$). This shows that younger children and older children did not respond to the different reward allocations in the same way, thereby replicating Blake & McAuliffe (2011). Accordingly, we performed all subsequent analyses of children's decisions separately by age group.

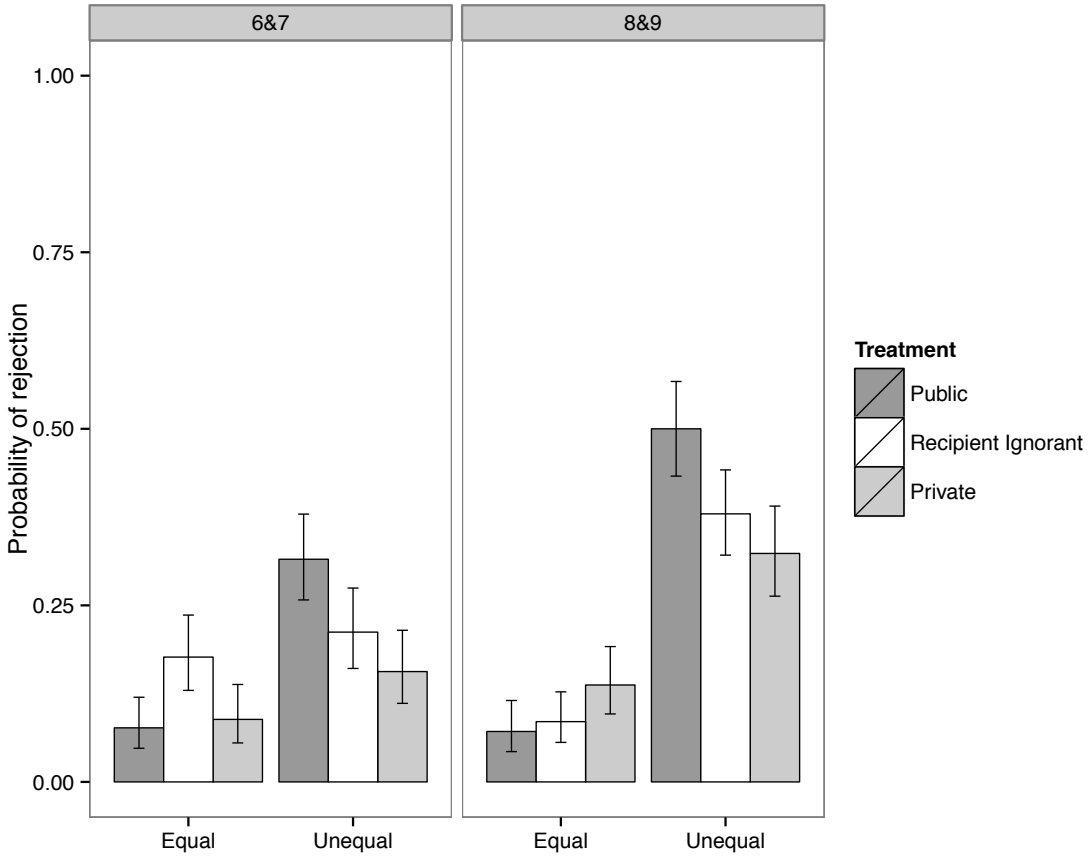

Figure 6.2. Bar plot generated from raw data showing probability of rejections of equal and unequal reward allocations in 6-7- and 8-9-year-old children across experimental treatments. Children received 6 equal trials (1 candy for decider and 1 candy for recipient) and 6 advantageously unequal trials (4 candies for the decider and 1 candy for the recipient). Children were assigned to one of three treatments: 1) Public, both the recipient and audience can see the decider's reward allocation; 2) Recipient Ignorant, the audience but not the recipient can see the decider's reward allocation; 3) Private, neither the audience nor the recipient can see the decider's reward allocation. Error bars indicate 95% confidence intervals.

Effect of audience on rejections in young (6-7-year-old) children

Figure 6.2 indicates that there is interaction between distribution and condition in 6-7-year-old children. Inspection of Fig. 6.2 shows that children rejected more unequal offers than equal offers in the Public but not in the Recipient Ignorant or Private conditions.

To test this statistically, we asked whether 6-7-year-olds were more likely to reject unequal offers in front of an audience than in private. Results from the minimal model are displayed in Table 6.2, showing two important predictors of children's behavior: 1) an interaction between distribution and condition ($X^2_2 = 20.87$, $P < 0.001$); and 2) an interaction between distribution and order ($X^2_1 = 7.7$, $P < 0.01$).

Table 6.2. Output from minimal generalized linear mixed model of 6-7-year-old children's decisions to accept (1) or reject (0) allocations of candy. Coefficients indicate the estimated effects of predictors on the response term relative to the following baselines: equal distribution; Public treatment and equal block first.

		β	s.e.	z	p	
	Intercept	3.17	0.44	7.29	0.00	***
Distribution	Unequal	-2.64	0.38	-6.91	0.00	***
Treatment	Private	-0.08	0.55	-0.15	0.88	
	Recipient Ignorant	-1.19	0.49	-2.42	0.02	*
Order	Unequal block first	0.05	0.41	0.12	0.90	
Distribution x Treatment	Unequal x Private	1.39	0.49	2.83	0.00	**
	Unequal x Recipient Ignorant	1.88	0.43	4.37	0.00	***
Distribution x Order	Unequal x Unequal block first	1.02	0.37	2.77	0.01	**

In the 6-7-year-old children, there was also a significant interaction between block order and distribution. Children who were given a block of six trials of equal reward allocations before a block of six trials of unequal allocations were more likely to differentiate between the offer types (they rejected more unequal offers than equal offers) than children who received the trial blocks in the opposite order (see Appendix 4, Fig. A4.1). This result suggests that receiving the equal trial block before the unequal trial block anchored children's expectations of the allocations, making them expect equality and thus more likely to reject the unequal offers that violated this expectation.

Effect of audience on rejections in older (8-9-year-old) children

To test our main hypothesis that older children would reject more unequal offers when making decisions in front of an audience compared to in private, we ran a GLMM of 8-9-year-olds' decision to accept or reject as the dependent measure and distribution, treatment, decider gender, recipient gender, order and interactions of interest as predictor variables. We then sequentially dropped terms from the full model to create a minimal model that only included terms whose exclusion would significantly decrease the model's fit. Results from the minimal model are shown in Table 6.3 and demonstrate that children's decisions to reject are related to two predictor variables: 1) the gender of the recipient ($X^2_1 = 5.08$, $P = 0.024$); and 2) a three-way interaction between decider gender x treatment x distribution ($X^2_2 = 7.85$, $P = 0.019$).

To explore the three-way interaction between gender x treatment x distribution, we plotted the raw data which are shown in Figure 6.3.

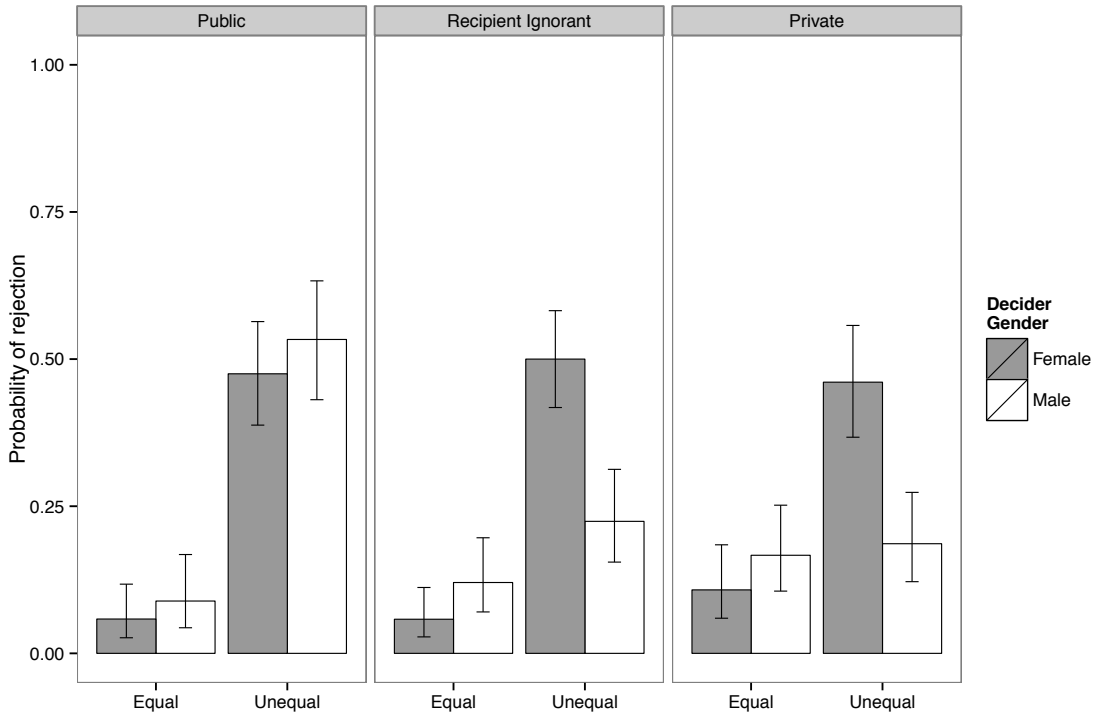

Figure 6.3. Bar plot generated from raw data showing probability of rejections of equal and unequal reward allocations in 8-9-year-old children. Bars show rejections by female deciders compared to male deciders across three experimental treatments. Children received 6 equal trials (1 candy for decider and 1 candy for recipient) and 6 advantageously unequal trials (4 candies for the decider and 1 candy for the recipient). Children were assigned to one of three treatments: 1) Public, both the recipient and audience can see the decider's reward allocation; 2) Recipient Ignorant, the audience but not the recipient can see the decider's reward allocation; 3) Private, neither the audience nor the recipient can see the decider's reward allocation. Error bars indicate 95% confidence intervals.

This figure shows that females rejected more unequal reward allocations than equal reward allocations across the three treatments. Thus, females showed an aversion to advantageous inequity even when making decisions that were hidden from the recipient and audience. Males, on the other hand, rejected more unequal allocations than equal allocations in the Public condition, where both the recipient and the audience could watch their decisions but tended to accept unequal allocations in the Recipient Ignorant and

Private conditions. Interestingly, males responded in the same way to the Recipient Ignorant and Private condition, suggesting that their partner's knowledge of the candy allocation, rather than exposure to an audience, drove their decisions to reject or accept.

Another significant predictor of children's decisions to accept or reject is the gender of the recipient (see Table 6.3).

Table 6.3. Output from minimal generalized linear mixed model of 8-9-year-old children's decisions to accept (1) or reject (0) allocations of candy. Coefficients indicate the estimated effects of predictors on the response term relative to the following baselines: equal distribution; Public treatment male actor gender and male recipient gender.

		β	s.e.	z	p	
	Intercept	3.4	0.57	6.01	0.00	***
Distribution	Unequal	-3.19	0.5	-6.32	0.00	***
Treatment	Private	-1.04	0.69	-1.52	0.13	
	Recipient Ignorant	-0.5	0.71	-0.70	0.48	
Actor Gender	Female	0.4	0.75	0.54	0.59	
Recipient Gender	Female	-0.67	0.29	-2.29	0.02	*
Distribution x Treatment	Unequal x Private	3.03	0.64	4.76	0.00	***
	Unequal x Recipient Ignorant	2.27	0.65	3.48	0.00	***
Distribution x Actor Gender	Unequal x Female	-0.05	0.7	-0.07	0.95	
Treatment x	Private x Female	0.14	0.98	0.14	0.89	
Actor Gender	Recipient Ignorant x Female	0.45	1.01	0.44	0.66	
Distribution x Treatment x	Unequal x Private x Female	-2.11	0.9	-2.34	0.02	*
Actor Gender	Unequal x Recipient Ignorant x Female	-2.44	0.94	-2.60	0.01	**

The negative coefficient associated with the recipient gender term in the minimal model shows that when subjects played with a female partner they were more likely to reject reward allocations of any distribution than those paired with a male recipient. Note that there was no significant interaction between recipient gender and distribution, meaning that subjects were not more likely to reject unequal offers when playing with a female partner but rather were more likely to reject both unequal and equal allocations when playing with a female partner compared to a male partner.

Male deciders' rejections across treatments echo the pattern of rejections seen in 6-7-year-old children, suggesting that from a young age children are sensitive to who is watching and are more likely to enforce costly fairness norms in front of an audience than in private. However, as children age, females' rejections of advantageous inequity diverge from males, and females begin to reject advantageous inequity regardless of who is watching.

Reaction time analyses

In addition to examining children's decisions to accept and reject different allocations of candies, we were interested in whether children took longer to make decisions about unequal versus equal offers. A longer reaction time when faced with advantageously unequal offers compared to equal offers would indicate that children are conflicted about their decisions. Furthermore, differences in reaction time across treatments in this study could highlight the factors that lead to internal conflict in children's decision-making about advantageous inequity.

To address these questions we first asked whether deciding to reject reward allocations took longer than deciding to accept reward allocations. Second, we asked whether decision times varied across treatments and across age groups. To examine which factors predicted children's reaction time we ran a full model with logged reaction time as a response term and distribution, decision, treatment, age group, decider gender, recipient gender, and interactions of interest as predictor variables. We then created a minimal model by sequentially removing terms from the full model such that the minimal model only included terms whose exclusion significantly reduced the fit of the model. Using this model, the interaction between distribution type and decision was the only significant predictor of reaction time ($X^2_1 = 5.82$, $P = 0.016$). Figure 6.4 illustrates this interaction and demonstrates that children in both age groups and across treatments took longer when deciding to reject as opposed to accept reward allocations.

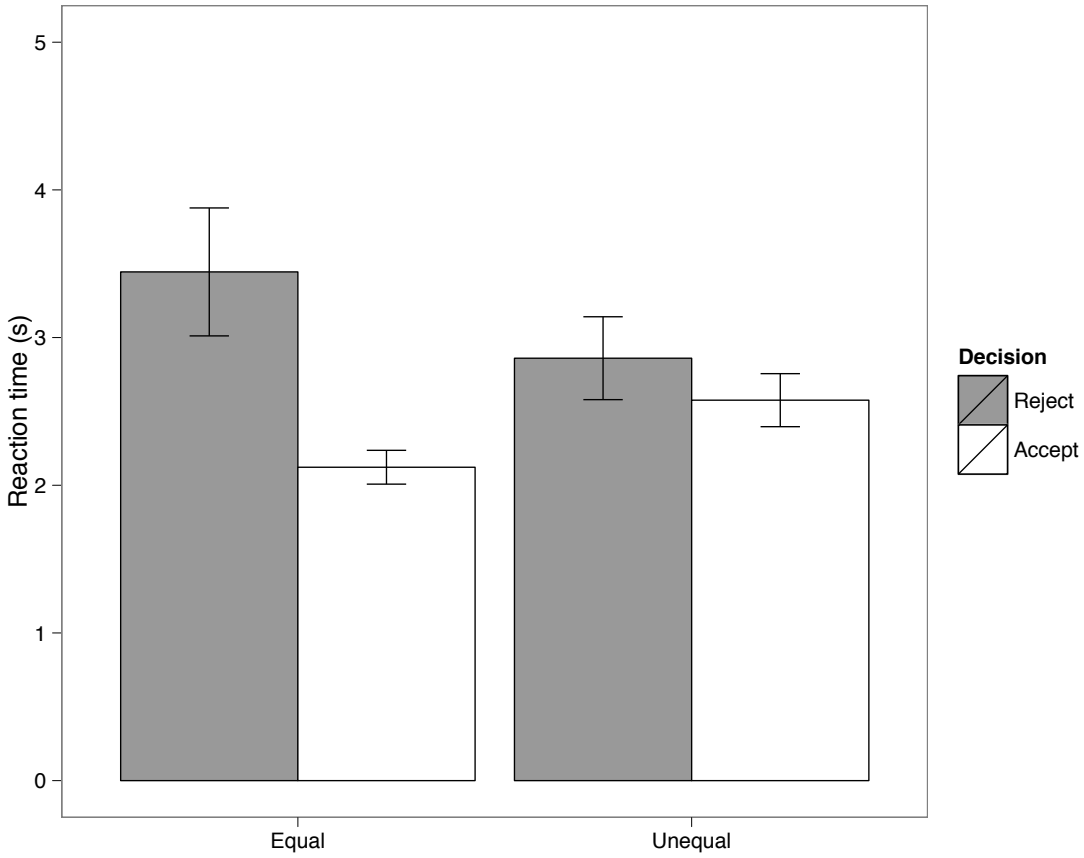

Figure 6.4. Bar plot of reaction time (s) data in 6-9-year-olds. Bars show reaction time by decision (accept or reject) and reward distribution (equal or unequal). Reaction times indicate the time it took children to decide to accept or reject reward allocations once a trial had been initiated. Children received 6 equal trials (1 candy for decider and 1 candy for recipient) and 6 advantageously unequal trials (4 candies for the decider and 1 candy for the recipient). Error bars indicate 95% confidence intervals.

However, this difference was differentially affected by distribution of rewards: children took longer to reject equal offers than to accept equal offers and this pattern also held for unequal offers but to a lesser extent. Thus, contrary to our predictions, older children did not appear to show longer reaction times when faced with advantageous inequity

compared to younger children. Furthermore, children's reaction time did not vary across experimental treatments.

DISCUSSION

The current study had three major results: (1) we replicated Blake and McAuliffe (2011); (2) we found effect of audience on advantageous inequity rejections; (3) we observed a gender effect in audience sensitivity in the older children.

In this study, we replicated the previously reported developmental shift in the onset of advantageous inequity aversion (Blake & McAuliffe, 2011). Children in the 8-9-yea-old age group were more likely to reject advantageously unequal reward allocations than were 6-7-year-old children.

There were two novel results. First, 6-7-year-olds were more likely to reject advantageously unequal offers when making decisions while being watched by their partner than when making decisions while hidden from their partner. Second, in 8-9-year-old children, boys showed this same sensitivity to being observed by their partner while girls consistently rejected more unfair resource allocations regardless of who was watching. Interestingly, neither 6-7-year-old children nor 8-9-year-old boys distinguished between the Recipient Ignorant and Private treatments, indicating that these children's rejections of unfair offers may have been motivated by a desire to meet their partner's expectation of fair behavior as opposed to the audience's expectations of fair behavior. Our study also found that children's reaction time on trials was related both to the reward

distribution as well as their ultimate decision to accept or reject a given allocation of candy but was not affected by experimental treatment.

While our results confirmed the expected age shift in rejections of advantageous inequitable offers, 6-7-year-old children in the Public treatment rejected advantageous allocations at a higher level than demonstrated in Blake & McAuliffe (2011). On average, children in the public treatment in the present study rejected about one more advantageous offer (out of 6) compared to the previous study. One possible reason for the difference between the two studies is that the current study asked children to examine the apparatus from both sides prior to participating in the task. This act of perspective taking may have increased the children's ability to think about how an advantageous reward allocation would be perceived by the recipient and thus may have increased the likelihood that they would reject these offers. Consistent with this idea is the result that perspective-taking abilities are known to influence children's decisions in the ultimatum game (Takagishi et al., 2010). Moreover, a similar result has been demonstrated in a study of adults' decisions in a version of the ultimatum game (Güth et al., 1996): players were more generous when they had been asked to answer pre-experimental questions that forced them to think about the game from the recipients' perspective.

If 6-7-year-olds' rejections of advantageous allocations were indeed sensitive to this inadvertent perspective-taking prime then it is possible that advantageous inequity is more generally vulnerable to extrinsic factors in younger children compared to older children. If so, this vulnerability could explain the order effect that was observed in the younger age group. Children in the 6-7-year-olds age group who received the equal trial block before the unequal block were more like to reject advantageously unequal offers

than children who received the blocks in the opposite order. Making decisions about the equal trials first, may have set up an expectation of equity, leading subjects to be more sensitive to deviations from equity compared to subjects who saw the unequal block of trials first.

The main result from our study is that children in the 6-7-year-old age group and male participants in the 8-9-year-old age group showed higher rejections of advantageous reward allocations in the Public treatment than in the Recipient Ignorant and Private treatments. In both groups, however, children were as likely to reject advantageous allocations in the Recipient Ignorant treatment as they were in the Private treatment. This suggests that these children were attending to whether or not their partner, a novel peer, could see their allocations and were not additionally concerned with whether the audience of onlookers could also see their allocations. This result is consistent with other work on the development of self-presentation that shows that as children age they become increasingly concerned with self-presentation before peers. Specifically, Watling and Banerjee (2007) showed that British children aged 8-11 judged modesty as more important for peer audiences than adult audiences. While our study was not addressing modesty, our result is consistent with their reported shift towards appealing to peers with age.

The finding that 6-7-year-old children and 8-9-year-old boys were sensitive to their partner points to a possible motivation for children's rejection of advantageous inequity. Through rejecting advantageous reward allocations, children may have been signaling to their partner that they are fair-minded with the aim (most likely unconscious) of gaining reputational benefits from doing so. Moreover, the fact that children were able

to mediate their rejections of advantageous allocations shows that they were sensitive to their partner's expectations of fairness. When they knew that their partner could not see their reward allocation, and thus could not have an expectation of fair behavior, they were more likely to accept advantageous reward allocations.

The result that children change their behavior to adhere to their partner's expectations of fairness is consistent with a result from a three-player version of the ultimatum game that was conducted with adults (Güth et al., 1996). We turn now to the adult literature because, to our knowledge, this type of manipulation has not been conducted with children. In this ultimatum game modification, Player One is able to offer a portion of an initial monetary endowment to Players Two and Three. If Player One's offer is accepted then Players Two and Three play a second Ultimatum Game with the offered money. If, on the other hand, Player One's offer is rejected, the game is terminated and no player receives any money. In Güth and colleagues' game, all players knew that the initial endowment could either be large or small, with a known probability. Critically, however, only Player One would know whether the original endowment was large or small in a given round of the game. Under these circumstances subjects in the role of Player One acted as if they knew that unfair offers would be rejected and thus manipulated the other players' beliefs about the amount of the original endowment. Even in a case of a large original endowment, Players Ones would offer a fair split of the small endowment amount, suggesting that they hoped to trick Player Twos into thinking that the original endowment had been small. More broadly, this result suggests that seemingly fair behavior in adults is motivated by a desire to meet others' expectations of fairness as opposed to an intrinsic desire for fair outcomes. This suggestion is in line with what we

observed in the younger age group and the older boys: these children rejected unequal allocations when being watched by a peer who most likely had an expectation that the decider would act fairly.

A key feature of the Inequity Game is that the children participating in the task did not know one another and were unlikely to interact with one another in the future. The fact that deciders and recipients did not know each other rules out the idea that deciders may have rejected advantageous allocations in order to increase the probability of direct reciprocity. Rather, any benefits individuals accrued through signaling to a novel peer would have been gained through indirect reciprocity (Nowak and Sigmund, 2005).

Our main hypothesis was that children are motivated to reject advantageous offers in order to gain reputational benefits from appearing fair, rather than because they are motivated by fairness per se. Results from the 6-7-year-olds and the 8-9-year-olds lend support. Critically, children appear to be willing to incur a relatively large cost in order to demonstrate to a peer that they adhere to norms of fairness. This result challenges the hypothesis that the expression of advantageous inequity aversion in children is purely due to the internalization of a strong norm of fairness in children. However, the gender difference observed in the older age groups suggests that a strong reputation-based account for the expression of advantageous inequity is also not warranted.

Our study showed that, unlike 8-9-year-old boys, girls in the older age group did not vary their rejections of advantageous inequity based on who could see them make decisions. This finding may indicate that by the age of eight girls, but not boys, have internalized a strong norm of fairness. This explanation would predict that boys would

eventually elicit the female-pattern of rigid rejection of advantageous inequity. Alternatively, boys in this age group may be more sensitive to self-presentation than girls and thus take a more socially strategic approach to rejections of advantageous inequity. This explanation would predict that girls would eventually elicit the male-pattern of flexible rejection of advantageous inequity aversion. A third alternative is that girls are more driven by reputational concerns and continue to reject advantageous allocations in the Recipient Ignorant and Private treatments because they were trying to appear fair to the experimenter, who could see their behavior at all times. Consistent with this third alternative, is that in Italian 5-15-year-olds, girls were less likely to cheat than boys when explicitly told in experimental instructions to be honest, although this was a weak effect (Bucciol and Piovesan, 2011). Furthermore, evidence suggests that children do attempt to appear fair in front of an experimenter (Shaw et al., in press). Although our results are consistent with the idea that girls attempted to appear fair before the experimenter, our results do not suggest that they only cared about the experimenter. Rather, it is likely that they cared about all members of the audience, including the experimenter. Future work could attempt to highlight which members of the audience (partner, experimenter or onlookers) most influence the expression of advantageous inequity aversion in girls.

One aspect of our study that can help distinguish between the alternative explanations for the observed gender difference in the 8-9-year-olds is the developmental trend demonstrated between the younger and the older children. The 8-9-year-old boys show patterns of rejection that would be consistent with the idea of advantageous inequity aversion emerging during development in tandem with reputational concerns. The 8-9-year-old girls' behavior would thus represent a deviation from this pattern. The

fact that the older girls deviate from the developmental pattern lends support to the idea that girls begin to internalize a strong norm of fairness with age and that this norm is impervious to audience effects. Thus, this pattern favors the first proposed explanation for the expression of advantageous inequity aversion in children.

Despite the developmental trend, we cannot clearly distinguish between the three proposed alternatives for the observed gender difference in advantageous inequity aversion in older children. Nevertheless, it is worth examining the observed gender-difference in the context of what we know about gender differences in adults' behavior in similar economic games. To our knowledge, no study has found gender difference in studies that explicitly tested advantageous inequity aversion in adults. However, in other social dilemmas, women are thought to be more socially-oriented and generous than men and men are thought to be more self-oriented than women (Eckel and Grossman, 1998; 2001; 2008). Furthermore, women tend to be more generous than men under conditions of high cost (Andreoni and Vesterlund, 2001). On the other hand, a meta analysis of gender differences in social dilemmas suggested that by adulthood men and women do not differ substantively in their cooperative tendencies (Balliet et al., 2011). Thus, the evidence for gender differences in generosity in economic games is mixed but where studies have demonstrated a gender difference, reported effects tend to be in the direction of greater generosity in women. Our results are consistent with the idea that women tend to be more generous than men, especially when costs are high. It is possible, therefore, that our game has captured the age at which these gender differences begin to emerge in Boston children. We view the further exploration of the origin of a gender difference in advantageous inequity aversion as a fruitful area for future inquiry.

A second gender effect that emerged from our study is that 8-9-year-old deciders were more likely to reject allocations of both equal and unequal distributions when paired with a female recipient. We cannot currently provide a firm explanation of this result, but it is intriguing to note that gender pairings have been shown to be important in adult studies of economic decision-making. In at least one study, female recipients were more likely to be the recipients of generosity than male recipients (Dufwenberg and Muren, 2006). What is puzzling about our finding, however, is that rejections were not specific to unequal reward allocations but were rather common to both equal and unequal. Future work should examine whether specific gender pairings affect children's propensity to reject advantageously unequal reward allocations or indeed whether gender pairing have broader effects on fairness preferences in children.

A final result from this study was that children showed longer reaction times when facing unequal reward allocations compared to equal allocations and when they were deciding to reject allocations as opposed to accept them. Their longer reaction time in these instances indicates that subjects were not simply reacting automatically to the different distributions but were rather thinking about their decisions when faced with different allocations (Piovesan et al., 2009; Rand et al., 2012). However, children did not show differences in reaction time across the three experimental treatments, suggesting that they were equally conflicted when faced with different reward distributions, regardless of who was watching them make decisions. The fact that children were not automatically rejecting advantageous allocations lends further support to the idea children were not simply acting on a previously internalized norm of fairness. Rather, our reaction

time data suggest that children's decisions about advantageous inequity tended to be calculated.

In sum, the current study provides evidence for a strong relationship between advantageous inequity aversion and reputation concerns in children ages 6-9. We found support for the hypothesis that reputational concerns about fairness are in place in the 6-7-year-olds. Children in this age group and 8-9-year-old boys were more likely to incur a cost to reject advantageous reward allocations when their partner was aware of the distribution of candy. Older (8-9-year-olds) girls, on the other hand, rejected unequal reward allocations regardless of whether or not their partner was watching. To our knowledge, ours is the first study to examine the relationship between the costly adherence to fairness norms and reputational concerns during child development. Our results point to intriguing patterns in the emergence of advantageous inequity aversion and suggest that there may be an important gender difference in its expression in older children.

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CHAPTER 7

GENERAL DISCUSSION

In this dissertation, I explored the evolutionary and developmental origins of inequity aversion. My findings contribute to a growing understanding of the expression of inequity aversion in nonhuman animals and its emergence during human ontogeny in three ways. First, they raise important questions about constraints on the expression of disadvantageous inequity aversion in animals and its specific role in cooperative relationships. Second, they provide evidence that different processes support disadvantageous and advantageous inequity aversion in humans. Third, they suggest that the occurrence of advantageous inequity aversion may be explained partially by reputational concerns.

In this discussion, I elaborate on the specific contributions of my dissertation research and situate my findings within the broader context that was reviewed in Chapter 2. I then highlight unanswered questions about the expression of inequity aversion in animals and children. Additionally, I outline weaknesses in the current conceptualization of inequity aversion and specifically, of its role in cooperative societies. Finally, I suggest how future work might address these weaknesses.

SUMMARY OF MAIN FINDINGS

Summary of Chapters 3 and 4: evolutionary origins of inequity aversion

In Chapters 3 and 4 I examined whether nonhuman animals react negatively to distributional inequity. Findings from Chapter 3 indicate that cotton top tamarins may show a weak aversion to inequality but that this aversion is present only when individuals must work for rewards. Although this effect was observed in five out of the seven subjects tested, only one individual exhibited a striking aversion to inequity when she had to exert effort to access rewards. I argue that given the potential role of individual differences in animals' responses to inequity, we must be careful to (1) report inequity aversion results by individual wherever possible and (2) exercise due caution when generalizing findings from experiments on laboratory animals to the species level.

In Chapter 4 I found that neither domestic dogs nor dingoes showed an aversion to unequal reward distributions. Individuals in both species were less likely to participate in an experimental task when they were not rewarded compared to when they were rewarded. However, reluctance to participate was independent of (1) whether a social partner was present and, by extension, (2) whether a social partner was being rewarded. This finding contradicts a previous study that showed that domestic dogs exhibit inequity aversion (Range et al., 2009). I suggest that this inconsistency may be due to methodological differences between my study and previous work. I argue that my method is more suitable for testing a wide range of individuals (within and between canid species) and that my result that subjects in my study did not show inequity aversion indicates that inequity aversion is not readily expressed in social canids.

Summary of Chapters 5 and 6: developmental origins of inequity aversion

Results from Chapter 5 showed that Boston children's rejections of inequity were not a signal to the experimenter. Subjects did not distinguish between unequal offers that had

been deliberately versus randomly generated. Findings also indicated that disadvantageous, but not advantageous, inequity aversion has an important nonsocial component in children. Subjects between the ages of 4- to 9-years-old rejected some disadvantageously unequal reward allocations when not paired with a social partner. However, children tended to reject such allocations at a higher rate when they are paired with a partner. By contrast, subjects did not reject advantageously unequal offers when not paired with a partner, indicating that advantageous inequity aversion is specifically social in children.

Findings from Chapter 6 speak directly to results from Chapter 5 by addressing the question of why advantageous inequity aversion is specifically social in children. Results showed that advantageous inequity aversion might, at least in part, be a costly signal. Children between the ages of six and nine rejected advantageously unequal offers when others were watching. Older girls continued to reject advantageous offers when they could do so in private. By contrast, boys tended to accept advantageously unequal offers in private and rejected them in public. These findings suggest that by the age of 8, reputational concerns drive rejections of advantageous inequity aversion in boys but not girls.

BROADER IMPLICATIONS

Are disadvantageous and advantageous inequity two sides of the same coin?

The current definition of inequity aversion as a willingness to "give up some material payoff to move in the direction of equitable outcomes" does not necessarily distinguish

between advantageous and disadvantageous inequity aversion (Fehr & Schmidt, 1999). However, mounting evidence from studies of (1) animals, (2) children and (3) adults suggests that different processes support these two forms of inequity aversion.

First, only one of more than twenty studies of animal inequity aversion has provided suggestive evidence that nonhuman species react to advantageous inequity aversion (Brosnan et al., 2010). In contrast, a number of animal studies have reported disadvantageous inequity aversion (Brosnan & de Waal, 2003; Brosnan et al., 2005; Fletcher, 2008; Neiworth et al., 2009; Range et al., 2009; Range et al., 2012; van Wolkenten et al., 2007). Although advantageous inequity aversion is seldom the target of animal research (presumably because researchers believe it is unlikely to be observed), most inequity aversion studies have inadvertently provided subjects with the opportunity to express intolerance of advantageous outcomes. In these studies, subjects typically receive rewards in the following sequence: a recipient receives (or has to work for) a high value food item and then the actor is presented with (or has to work for) a low value food item (see Chapter 2, Part 3 for a review of animal inequity aversion studies). Given that subjects in these tasks are tested over multiple trials, recipients – the beneficiaries of unequal distributions – could, in principle, cease to participate in the task. If they did this, their behavior would be consistent with advantageous inequity aversion. To my knowledge, this has never been reported.

Second, advantageous inequity aversion emerges later in child development than disadvantageous inequity aversion (Blake & McAuliffe, 2011; Shaw & Olson, 2012). Moreover, advantageous inequity aversion appears to be expressed solely in social contexts while disadvantageous inequity aversion is expressed in both social and

nonsocial contexts (Chapter 5). These findings suggest that children do not perceive deviations on either side of equality to be equally egregious. Indeed, until around the age of eight, children readily accept advantageous, but not disadvantageous, inequity.

Third, adults show an asymmetry in their tolerance of disadvantageous and advantageous inequity aversion: people tend to be less tolerant of disadvantageous inequity (Loewenstein et al., 1989).

These three converging lines of evidence support the existing argument that we should treat advantageous and disadvantageous inequity aversion as different processes (Blake & McAuliffe, 2011; Shaw & Olson, 2012). I therefore address them each independently here.

Advantageous inequity aversion

Is advantageous inequity aversion special?

Inequity aversion appears to be procedurally and developmentally distinct from disadvantageous inequity aversion. However, it is not clear that this distinction sets it apart from other processes that guide social decision-making in humans.

For instance, is advantageous inequity distinct from the process that promotes generosity in humans? At surface value, generosity in games such as the dictator game is consistent with an aversion to advantageous outcomes: individuals sacrifice personal gain to avoid an advantageously unequal reward distribution. If these are indeed the same process, then why does advantageous inequity aversion emerge late in development while spontaneous generosity emerges relatively early (Benenson et al., 2007; Blake & Rand, 2009)?

It is possible that this inconsistency arises from differences in tasks designed to test generosity compared to those designed to test inequity aversion. For example, in the Inequity Game discussed in Chapters 5 and 6, inequity aversion is measured by children's propensity to prefer *no rewards* to an unequal reward distribution. In contrast, in the dictator game, children invariably receive something but their ultimate payoff depends on generosity. The difference between 'fewer' rewards and 'no' reward may be more important to younger children than to older children. If this is true, it could explain the conflicting results between the dictator game and the Inequity Game. Alternatively, the early emergence of generosity in the dictator game may be due to the fact the children enjoy being in charge of distributing resources.

Future work could test these ideas by manipulating (1) who has control over resources and (2) the degree of inequity between two individuals.

Disadvantageous inequity aversion

Is disadvantageous inequity aversion specifically social?

Compared to advantageous inequity aversion, disadvantageous inequity aversion appears to have deep roots in development (Blake & McAuliffe, 2011; LoBue et al., 2011). Furthermore, some nonhuman animals show an aversion to disadvantageous reward allocations (Brosnan & de Waal, 2003; Brosnan, et al., 2005; Fletcher, 2008; Neiworth et al., 2009; Range et al., 2009; Range et al., 2012; van Wolkenten, et al., 2007). These findings, combined with results that show that disadvantageous inequity aversion is widespread across human populations (Henrich et al., 2005), suggest that humans'

aversion to disadvantageous reward distributions may be an evolved trait as opposed to a trait inherited exclusively through socio-cultural pathways.

Given this, it is reasonable to ask whether existing evidence for disadvantageous inequity aversion across species can inform our understanding of how it evolved. Specifically, does existing evidence support the Social or Nonsocial Hypothesis for the evolution of inequity aversion?

The Social Hypothesis proposes that inequity aversion evolved *for* cooperation and, as such, is specifically social (Brosnan, 2006, 2011). According to this hypothesis, inequity aversion evolved as a mechanism for the regulation of relative investments in, and payoffs from, cooperation. The Nonsocial Hypothesis, on the other hand, proposes that inequity aversion may be used in cooperation but did not necessarily evolve for cooperation (Chen & Santos, 2006). According to this hypothesis, inequity aversion may be exhibited in both nonsocial and social contexts.

I argue that existing evidence for the expression of disadvantageous inequity aversion in humans and nonhuman animals is more consistent with the Nonsocial Hypothesis than the Social Hypothesis. This argument is grounded on two main findings: (1) individuals reject inequity in the absence of work effort and (2) individuals reject inequity in nonsocial contexts.

Although effort clearly influences the expression of inequity aversion (Adams, 1963, 1965), it is not a necessary prerequisite of inequity aversion in adults (Dawes et al., 2007; Takagishi et al., 2009), children (Blake & McAuliffe, 2011; Shaw & Olson, 2012) or animals (Range et al., 2009). If inequity aversion evolved specifically for cooperation, it is unlikely that it would be expressed in situations where a work-to-payoff ratio is

irrelevant. A possible counter-argument to this idea is that inequity aversion may have evolved for cooperation, but is occasionally - or even routinely - misapplied in non-cooperative situations. In other words, individuals' responses to disadvantageous inequality are so potent that they are generalized to contexts where resources are simply distributed unequally between individuals. By this account, inequity aversion is specifically social, but can be elicited outside of the domain of cooperation. If this were the case then one would expect inequity aversion to be expressed only where resources are distributed among individuals.

Contrary to this prediction, individuals reject unequal outcomes even when they are not interacting with a social partner. Indeed, nonsocial rejections have been documented in adults (Sanfey et al., 2003), children (Chapter 5) and animals (Chapter 4; Brauer et al., 2006; Brosnan & de Waal, 2003; Brosnan, et al., 2005; Dubreuil et al., 2006).

The finding that humans and animals reject disadvantageously unequal reward allocations in cases where outcomes are not dependent on collaborative effort and in nonsocial contexts, suggests that individuals have a *general* aversion to disadvantageous inequity. Given this, inequity aversion may have evolved from general mechanisms that allow individuals to track resources relative to those of other individuals and of those available in a given environment (Chen & Santos, 2006; Kahneman & Tversky, 1979; Tversky & Kahneman, 1981).

Are "nonsocial" controls truly nonsocial?

The argument outlined above hinges on evidence that individuals are willing to reject inequitable reward allocations in "nonsocial" situations. However, in studies of animals and children, these nonsocial situations still involve an experimenter, who is typically responsible for distributing rewards. Thus, rejections in these contexts could be interpreted as a signal to experimenters.

In Chapter 5, I directly addressed this question by asking whether children's rejections in the inequity game were a signal to the experimenter. Results showed that children were not sensitive to the origins of allocations (i.e. deliberate or random) and instead were focused on the unequal reward outcomes. Given this result, it is unlikely that rejections in the nonsocial game were driven by a desire to signal to the experimenter.

Similar manipulations of the experimenter's role as a reward distributor have not yet been conducted in animal studies on inequity aversion. As such, we cannot rule out the possibility that rejections of inequity in animal tasks are a signal to experimenters. Future work could test this possibility by arranging for subjects to interact with an apparatus that is not (or at least not obviously) controlled by an experimenter. For example, drawing on the token exchange paradigms that are common in studies on animal inequity aversion (Brauer et al., 2009; Brosnan & de Waal, 2003; Brosnan, et al., 2005; Silberberg et al., 2009; van Wolkenten, et al., 2007), one could train subjects to dispense tokens into an apparatus that automatically provides rewards in return. The apparatus could automatically distribute either equitable or inequitable reward allocations to pairs of subjects. If subjects continued to exhibit inequity aversion when interacting with this type of apparatus, we would have strong evidence that their rejections are not a signal to experimenters. Until manipulations of this nature are able to rule out the

potentially confounding effect of signaling, we must interpret results of rejections in both social and nonsocial conditions with caution.

Is inequity aversion used for cooperation in animals?

Given the lack of evidence that inequity aversion is *specific* to cooperation in animals, perhaps a simpler is question is: to what extent is inequity aversion *used* in cooperation? To date, all experimental tests of inequity aversion in animals have been conducted on captive individuals. These studies have invariably tested subjects on tasks in which they make decisions about relative distributions of food items. This method provides a test of inequity aversion that is roughly equivalent to the types of tests conducted on human subjects using money as a currency. However, a major limitation of these tasks is that they lack ecological relevance for the subjects being tested. Most cooperation in animals occurs in domains other than food sharing (Dugatkin, 1997). Thus, even if animals do respond to inequities in cooperative relationships, present paradigms are unlikely to capture their natural responses. Only one study to date has tested inequity aversion in a species (cleaner fish, *Labroides dimidiatus*) that routinely cooperates in the foraging domain, and it found no evidence for inequity aversion (Raihani et al., 2012).

My own study on cotton top tamarins (*Saguinus oedipus*, Chapter 3) is a relevant example of how experimental tests of inequity aversion are not typically designed with a species' ecology in mind. Cotton top tamarins are a cooperatively breeding species in which a breeding pair receives help from other individuals. For example, helpers invest in caring for the breeding pairs offspring by carrying infants on their backs. Given the costs associated with this cooperative behavior it is possible that individuals would benefit

from tracking their time-spent-carrying in relations to others' investments in carrying. Thus, an inequity aversion task that manipulated how long different helpers were able to contribute to offspring carrying would be more ecologically valid than a task that asks if they are averse to differences in relative quantities of food.

Is inequity aversion used for cooperation in humans?

Despite the wealth of evidence suggesting that humans show a strong aversion to inequity, we have little evidence that inequity aversion plays a role in sustaining cooperation in human societies. Although this idea has received theoretical support (Fehr & Schmidt, 1999), few empirical studies have highlighted inequity aversion per se as a key factor in individuals' cooperative decisions. Indirect evidence that inequity aversion may be used in cooperation comes from Raihani and McAuliffe (2012) who show that inequity aversion motivates punishment in humans. Given that punishment may play a key role in stabilizing cooperation in human societies (Boyd & Richerson, 1992), it is reasonable to think that inequity aversion may be used in cooperation in so far as it promotes punishment. However, to my knowledge no study has tested this idea.

Results from public goods games show that individuals punish low contributors (Fehr & Gächter, 2000). However, it is unclear whether punishment in these games is motivated by an aversion to distributional inequity or by a desire for retribution. In order to distinguish between these motivations, I suggest a public goods game that holds defection (i.e. no contribution to the public good) constant while varying distributional outcomes among players. A four-player version of the game could be structured as follows: Players 1 and 2 are initially endowed with $10. Players 3 and 4 are endowed

with $8. Players learn that any contributions to the public good will be doubled and distributed equally among the four players. Imagine that Players 1 and 2 decide to each contribute $2. Players 3 and 4 defect, and contribute nothing. In this scenario, the public good is thus $8 ($4 in contributions x 2). When the public good is distributed, all players end up with an equal payoff of $10.

If punishment is motivated by a desire to punish defectors (and to thus encourage cooperation in future rounds (Fehr & Gächter, 2002; Raihani et al., 2012), Players 1 and 2 will be motivated to punish Players 3 and 4. If, on the other hand, punishment is motivated by inequity aversion, no players will be motivated to punish.

Experiments such as this could help to distinguish individuals' motivations for punishment in cooperative games and help elucidate the role of inequity aversion in cooperation.

Uniting evolutionary and developmental perspectives

My dissertation research investigated the origins of inequity by using both a developmental and comparative perspective. While pursuing slightly different questions, these approaches inform each other in important ways. For example, as discussed in Chapter 5, studies of inequity aversion in children have adopted methodologies (e.g. nonsocial controls) that were developed to study animals.

An important question that has emerged from this dual-focused approach is the extent to which developmental factors might influence the expression of inequity aversion in animals. Given the cross-cultural variation observed in humans' fairness preferences (Henrich, et al., 2005) it is clear that the development of fairness requires

input from the social world. My thesis has examined these inputs in one population of children, and until cross-cultural developmental work is done, conclusions about the ontogeny of inequity aversion must be limited to the population I studied.

However, when interpreting results from animal studies, researchers readily generalize from the laboratory to the wild and from a small sample of captive subjects to the species level. While it is reasonable to think that animal social behavior shows less variation than that seen across different human populations, I argue that we should seek to characterize inter-individual and inter-group variation in animal inequity aversion. In Chapter 3 I suggest that one way in which we can begin to achieve this is by reporting results by individual.

One source of inter-individual or inter-group variation could be the environments in which animals are raised. In Chapter 4 I argue that a possible explanation for results showing that dogs are averse to inequity is that they have been trained to expect equality. This training explanation could equally apply to groups of captive laboratory animals. For example, if animals in a laboratory colony are raised in an environment in which they are fed equal amounts of food by a human experimenter, they may develop an expectation of equality.

Understanding whether developmental factors influence the expression of inequity aversion in animals could help reconcile the different results reported across research groups testing the same species on seemingly similar tasks (Brauer et al., 2009; Brosnan & de Waal, 2003; Brosnan, et al., 2005; Silberberg, et al., 2009).

Conclusions

Results from my thesis suggest that there are important differences between advantageous and disadvantageous inequity aversion. However, it is currently unclear whether either disadvantageous or advantageous inequity aversion is itself a distinct process. Advantageous inequity may be indistinguishable from altruistic sharing outside of laboratory tests while disadvantageous inequity aversion may be derived from other mechanisms for resource tracking.

Inequity aversion was formalized as a concept to describe patterns of behavior in cooperative interactions (Fehr & Schmidt, 1999). Since then, the concept has gained inertia and work on inequity is pervasive in the social sciences. I worry, however, that the explosion of work on inequity aversion has shifted our focus from viewing it as a way of describing behavior toward a more binary perspective, in which inequity aversion is either present or absent in different individuals or species. Furthermore, predominant theory states that inequity aversion is a key ingredient to human cooperation yet there is little direct evidence that demonstrates its role in cooperative interactions.

In order to make progress in understanding the origins of distributive justice we must break inequity aversion down to its constituent parts and rebuild the concept from a perspective grounded in social ecology.

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APPENDIX 1: SUPPLEMENTARY TABLES AND FIGURES FOR CHAPTER 3

Table A1.1. Table showing actor sex, age and recipients with whom they were paired. Cases where actor and recipient roles were switched were separated by at least two weeks to reduce the possibility of direct reciprocal behavior. Individuals were not related to one another except in the cases demarked by stars.

Actor	Sex	D.O.B	Recipients						
EM	Female	12/01/1992	DW	JM	PJ	RA	SD		
LS	Female	05/30/2001	DW	JM	PB	PJ*	RA*	RK	
PJ	Male	03/09/2000	DG	EM	JK	RB	SH		
RA	Male	05/30/2001	EM	JK	LG	RB	SH		
RB	Female	05/16/1996	DW	JM	PJ	RA	RK	SD	
SD	Male	07/25/2001	DG	EM	LG	RB	SH		
SH	Female	10/01/1994	DW	JM	PB	PJ	RA	RK	SD

- PJ and RA were LS's siblings

Table A1.2. Raw data for each subject across conditions. Fractions represent the number of times a subject pulled the tool out of 12 trials during a given session. Subjects were paired with a different recipient during each experimental block. During each block, subjects were tested on all three experimental conditions in counterbalanced order. Note that two sessions had fewer than 12 total trials (EM, block 1 and SD, block 5) due to invalid trials. Conditions were as follows: 1) Inequity (INEQ), actor received 1 piece of food, recipient received 4 pieced of food and the tool was not weighted; 2) Weighted Inequity (INEQ-W), actor received one piece of food, recipient received four pieces of food and a weight was attached to the tool; Weighted Non-social Control (NSC-W), actor receives one piece of food, while four pieces of food are placed on absent recipient's tray and a weight is attached to the tool.

Subject	Block	INEQ	INEQ-W	NSC-W
EM	1	11/11	12/12	12/12
	2	12/12	12/12	12/12
	3	12/12	12/12	12/12
	4	12/12	11/12	12/12
	5	12/12	12/12	12/12
LS	1	12/12	11/12	12/12
	2	12/12	12/12	12/12
	3	12/12	12/12	12/12
	4	12/12	12/12	12/12
	5	12/12	12/12	12/12
	6	12/12	12/12	12/12
PJ	1	12/12	11/12	12/12
	2	12/12	12/12	12/12
	3	11/12	12/12	11/12
	4	11/12	9/12	12/12
	5	12/12	12/12	12/12
RA	1	12/12	12/12	12/12
	2	12/12	12/12	12/12
	3	11/12	12/12	12/12
	4	12/12	12/12	12/12
	5	12/12	10/12	12/12
RB	1	12/12	12/12	10/12
	2	11/12	12/12	12/12
	3	12/12	12/12	12/12
	4	12/12	12/12	12/12
	5	12/12	12/12	12/12
	6	12/12	12/12	12/12

Table A1.2. (Continued)

Subject	Block	INEQ	INEQ-W	NSC-W
SD	1	12/12	12/12	12/12
	2	11/12	12/12	12/12
	3	12/12	11/12	12/12
	4	12/12	12/12	12/12
	5	10/10	12/12	12/12
SH	1	12/12	4/12	11/12
	2	11/12	5/12	12/12
	3	11/12	11/12	12/12
	4	11/12	11/12	10/12
	5	11/12	6/12	10/12
	6	10/12	10/12	12/12
	7	11/12	9/12	12/12

Table A1.3. Output from null and minimal generalized linear mixed models predicting tool pulling in subjects (N = 7). In the null model (A), pull (yes or no) was predicted by the random effects of subject and trial (condition INEQ-W and NSC-W, INEQ set as baseline).

	Term	Variance	S.D.	β	s.e.	z	p
(A) Null model:							
Random Effects	Trials|Subject	0.94	0.97				
	Subject	1.25	1.12				
(B) Full model:							
Random effects	Trials|Subject	1.14	1.07				
	Subject	1.36	1.17				
Fixed effects							
	Intercept			5.1	0.59	8.59	< 0.001
	Condition						
	INEQ-W			-1.45	0.38	-3.83	< 0.001
	NSC-W			0.47	0.5	0.94	0.347

Table A1.4. Output from null and minimal linear mixed models predicting logged reaction time subjects (N = 7). In the null model (A), logged reaction time was predicted by the random effects of subject and trial (condition INEQ-W and NSC-W, INEQ set as baseline).

	Term	Variance	S.D.	β	s.e.	t
(A) Null model:						
Random Effects	Trials|Subject	0.02	0.12			
	Subject	0.11	0.33			
(B) Full model:						
Random effects	Trials|Subject	0.02	0.12			
	Subject	0.11	0.33			
Fixed effects						
	Intercept			-1.11	0.13	-8.54
	Condition					
	INEQ-W			0.09	0.04	2.17
	NSC-W			0.09	0.04	2.22

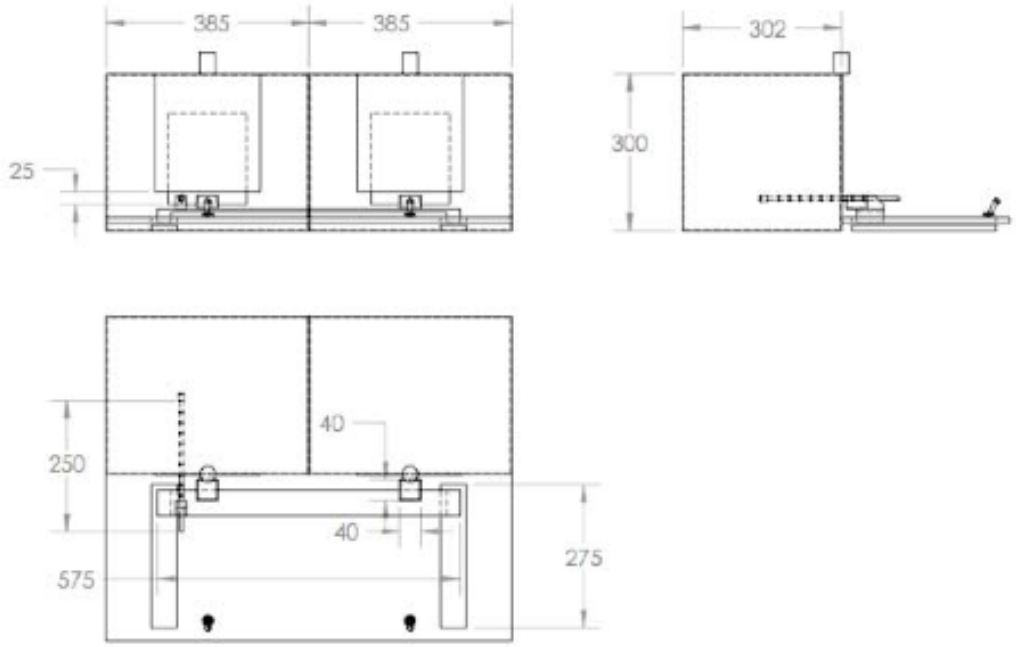

Figure A1.1. Diagram showing specific measurements of the apparatus (mm)

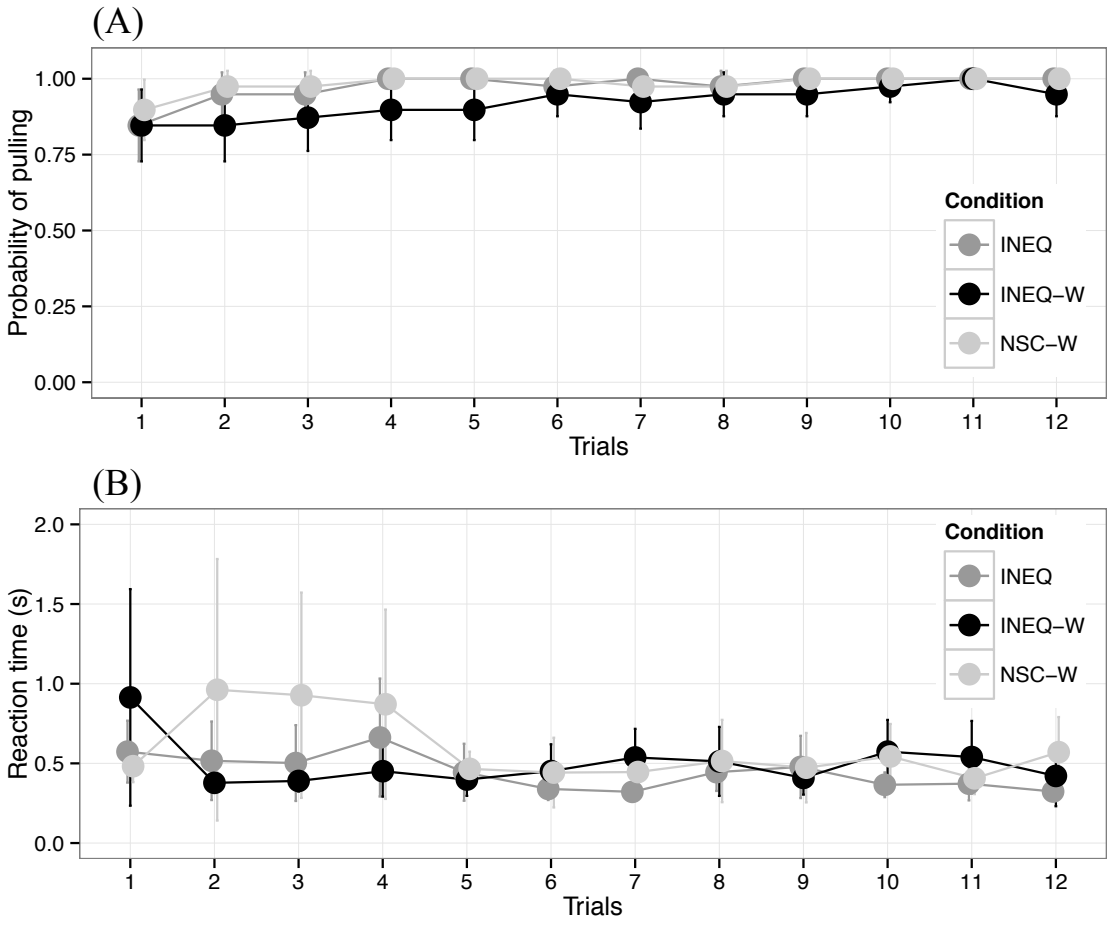

Figure A1.2. Line graph showing the probability of pulling the tool (A) and reaction time (B; time between gate opening and the initiation of a tool pull) across trials and between conditions: 1) Inequity (INEQ), actor received 1 piece of food, recipient received 4 pieced of food and the tool was not weighted; 2) Weighted Inequity (INEQ-W), actor received one piece of food, recipient received four pieces of food and a weight was attached to the tool; Weighted Non-social Control (NSC-W), actor receives one piece of food, while four pieces of food are placed on absent recipient's tray and a weight is attached to the tool. Error bars show 95% confidence intervals.

APPENDIX 2: SUPPLEMENTARY TABLES AND FIGURES FOR CHAPTER 4

Table A2.1. Breed, sex and condition information for dog subjects

Subject Name	Breed	Sex	Control Group	Confederate Partner	Day 1 Condition	Day 2 Condition
Angus	Irish Wolfhound	M	NSNR	Taaka	INEQ	NSNR
Annie	Pointer/Hound Mix	F	SNR	Stringer	SNR	INEQ
Ariel	Bernese Mountain Dog	F	SNR	Stringer	SNR	INEQ
Belichick	Puggle	F	NSNR	Stringer	NSNR	INEQ
Bergamot	Standard Poodle	F	NSC2	Taaka	INEQ	NSC2
Byron	Beagle	M	NSNR	Taaka	NSNR	INEQ
Chloe	Labradorrador	F	NSNR	Taaka	INEQ	NSNR
Cleo	Newfoundland	F	NSC2	Taaka	INEQ	NSC2
Clover	Goldendoodle	F	SNR	Stringer	SNR	INEQ
Clytie	Pembroke Welsh Corgi	F	NSNR	Taaka	INEQ	NSNR
Curley	Mix	M	SNR	Stringer	SNR	INEQ
Daisy1	Norwich Terrier	F	NSC1	Taaka	INEQ	NSC1
Daisy3	Greyhound/Labrador Mix	F	SNR	Stringer	INEQ	SNR
Danko	Black Mouth Cur	M	NSC1	Taaka	NSC1	INEQ
Dayton	Labrador/Golden Poodle	M	NSC2	Taaka	NSC2	INEQ
Diego	Portuguese Water Dog	M	SNR	Taaka	INEQ	SNR
Duke	Husky/Boxer	M	NSC1	Stringer	NSC1	INEQ
Ebony	Labrador/Beagle	F	NSC1	Taaka	NSC1	INEQ
Elzi	Shepherd Mix	F	NSC1	Taaka	INEQ	NSC1
Georgie	Labrador	M	NSC2	Taaka	NSC2	INEQ
Gilligan	Labrador Mix	M	NSC2	Taaka	NSC2	INEQ
Gracie	Dachshund	F	NSC1	Stringer	INEQ	NSC1
Gretchen	German Shepherd	F	NSC1	Stringer	INEQ	NSC1
Gromit	Border Collie	M	NSC1	Taaka	NSC1	INEQ
Gus	Cockapoo	M	NSC1	Stringer	INEQ	NSC1
Harry	Tibetan Terrier	M	SNR	Taaka	INEQ	SNR
Hawkeye	Border Collie	M	SNR	Stringer	SNR	INEQ
Honey	Golden Retriever	F	NSNR	Stringer	INEQ	NSNR
Hugo	Border Terrier	M	NSC1	Taaka	NSC1	INEQ
Jake	Puggle	M	NSC2	Stringer	INEQ	NSC2
Juno	Siberian Husky	F	SNR	Stringer	SNR	INEQ
Kapakahi	Foxhound	F	NSC1	Taaka	INEQ	NSC1
Kyler	Pembroke Welsh Corgi	M	NSC2	Taaka	NSC2	INEQ
Kyra	Rhodesian Ridgeback Mix	F	SNR	Stringer	INEQ	SNR
Lily	Bernese Mountain Dog	F	NSNR	Taaka	INEQ	NSNR
Lindy	Golden Retriever	F	NSNR	Stringer	INEQ	NSNR
Loki	Shiba Inu Mix	F	SNR	Taaka	INEQ	SNR
Louis	Mix	M	NSNR	Stringer	NSNR	INEQ
Lucy	Shepherd Mix	F	NSC2	Taaka	NSC2	INEQ
Luna1	Labrador Mix	F	NSC1	Taaka	INEQ	NSC1
Luna2	Border Collie	F	NSNR	Taaka	INEQ	NSNR

Table A2.1. (Continued)

Subject Name	Breed	Sex	Control Group	Confederate Partner	Day 1 Condition	Day 2 Condition
Mac	Border Collie	M	NSC2	Stringer	INEQ	NSC2
Mackenzie	Scottish Terrier	M	SNR	Stringer	INEQ	SNR
Maggie1	Cocker Spaniel	F	NSC1	Stringer	NSC1	INEQ
Maggie2	Labrador	F	NSC1	Taaka	INEQ	NSC1
Mai	Pit Bull Mix	F	NSC2	Taaka	NSC2	INEQ
Nunu	Great Pyrenees	F	SNR	Stringer	INEQ	SNR
Obikai	Pomeranian	M	SNR	Stringer	SNR	INEQ
Olivia	Cocker Spaniel	F	SNR	Stringer	INEQ	SNR
Omni	Rat Terrier	F	SNR	Stringer	INEQ	SNR
Oonah	Malamute	F	NSC2	Taaka	INEQ	NSC2
Papita	Papillion	F	NSNR	Taaka	INEQ	NSNR
Piper	Mutt/Shelter	F	NSNR	Taaka	INEQ	NSNR
Ponder	Cockapoo	M	NSNR	Taaka	NSNR	INEQ
Riley	Springer Spaniel	M	NSNR	Stringer	INEQ	NSNR
Rose	Border Terrier	F	NSNR	Taaka	INEQ	NSNR
Rosie1	Terrier Mix	F	NSC1	Taaka	INEQ	NSC1
Rosie2	Carolina Dog	F	NSC2	Taaka	INEQ	NSC2
Roxanne	German Shepherd	F	NSC2	Taaka	NSC2	INEQ
Ruby	Labrador/Terrier Mix	F	SNR	Stringer	SNR	INEQ
Sammie	Chow Mix	F	NSC2	Taaka	NSC2	INEQ
Sass	Labrador	F	SNR	Stringer	SNR	INEQ
Sioux	Australian Shepherd	F	NSNR	Taaka	NSNR	INEQ
Slipper	Labrador/Hound Mix	M	NSC2	Taaka	INEQ	NSC2
Snickers	Labradoodle	F	SNR	Stringer	SNR	INEQ
Spec	Jack Russell	M	NSNR	Taaka	NSNR	INEQ
Spot	Parson Russell Terrier	M	NSC2	Stringer	NSC2	INEQ
Sweetums	Bulldog	F	NSC1	Taaka	NSC1	INEQ
Sydney	Mix	F	NSC1	Taaka	NSC1	INEQ
Tahdy	Portuguese Water Dog	F	NSNR	Stringer	NSNR	INEQ
Tessie	German Shepherd	F	NSNR	Taaka	NSNR	INEQ
Nezumi	German Shepherd	F	NSC1	Taaka	NSC1	INEQ

Table A2.2. Sex and condition information for dingo subjects

Subject Name	Sex	Confederate	Day 1 Condition	Day 2 Condition	Day 3 Condition	Day 4 Condition	Day 5 Condition
AyJay	F	Deedee	INEQ	NSC2	NSC1	NSNR	SNR
Fanta	F	Deedee	NSNR	NSC2	SNR	INEQ	NSC1
Minka	F	Deedee	NSNR	SNR	NSC2	NSC1	INEQ
Opal	F	Deedee	SNR	NSC1	NSNR	INEQ	NSC2
Petal	F	Deedee	SNR	NSNR	NSC1	NSC2	INEQ
Rosie	F	Deedee	NSC1	INEQ	SNR	NSC2	NSNR
Snapple	M	Deedee	SNR	NSNR	NSC1	NSC2	INEQ
Tilly	F	Deedee	NSC2	INEQ	NSNR	NSC1	SNR
Wirra	F	Deedee	NSC2	NSNR	INEQ	SNR	NSC1
Yaouk	M	Deedee	INEQ	NSC1	NSC2	SNR	NSNR
Yoori	M	Deedee	NSC1	SNR	INEQ	NSNR	NSC2

Table A2.3. Output from a minimal generalized linear mixed model predicting approach behavior in dogs during the test half of sessions. In this model, approach (yes or no) is predicted by session type (control or inequity; control set as baseline), control group (NSNR, SNR, NSC1, NSC2; NSC2 set as baseline) and the interaction between session type and control group.

		β	s.e.	z	p	
	Intercept	0.15	0.32	0.46	0.644	
Session Type	INEQ	0.42	0.22	1.95	0.052	.
Control Group	NSNR	0.8	0.44	1.82	0.069	.
	SNR	1.24	0.44	2.8	0.005	**
	NSC1	0.86	0.45	1.93	0.054	.
Session Type x Control Group	INEQ x NSNR	-0.19	0.3	-0.62	0.538	
	INEQ x SNR	-0.86	0.3	-2.82	0.005	**
	INEQ x NSC1	-0.47	0.3	-1.57	0.117	

Table A2.4. Output from a minimal generalized linear mixed model predicting subject-to-experimenter referencing behavior in dogs during the test half of sessions. In this model, reference (yes or no) is predicted by session type (control or inequity; control set as baseline), control group (NSNR, SNR, NSC1, NSC2; NSC2 set as baseline) and the interaction between session type and control group.

		β	s.e.	z	p	
	Intercept	-2.41	0.38	-6.35	< 0.001	***
Session Type	INEQ	0.78	0.29	2.64	0.008	**
Control Group	NSNR	1.33	0.49	2.73	0.006	**
	SNR	1.03	0.49	2.12	0.034	*
	NSC1	-0.05	0.52	-0.1	0.921	
Session Type x Control Group	INEQ x NSNR	-1.3	0.37	-3.48	< 0.001	***
	INEQ x SNR	-1.2	0.37	-3.22	0.001	**
	INEQ x NSC1	-0.42	0.41	-1.02	0.31	

APPENDIX 3: SUPPLEMENTARY TABLES AND FIGURES FOR CHAPTER 5

Table A3.1. Number of children who participated in Studies 1 and 2. Table shows participant numbers by Study, Condition (*DI* Disadvantageous Inequity, *AI* Advantageous Inequity), Age Group, and Actor Gender (*F* Female, *M* Male).

		4&5		6&7		8&9		Total
		F	M	F	M	F	M	
Study 1: Deliberate versus Random	DI	7	13	10	14	9	11	64
	AI	12	9	10	9	11	9	60
Study 2: Nonsocial	DI	22	20	23	13	10	10	98
	AI	19	18	13	22	20	11	103

Table A3.2. Output from minimal generalized linear mixed model of subjects' decisions in the disadvantageous and advantageous inequity conditions of Study 1. Coefficients indicate the estimated effects of predictors on the response term (accept = 1, reject = 0) relative to the following baseline levels: Distribution = equal; Age group = 4&5-year-old; Actor gender = female.

Study 1			β	s.e.	z	p
Disadvantageous Inequity		Intercept	3.43	0.69	5.00	< 0.001
	Distribution	Unequal	-3.55	0.68	-5.24	< 0.001
	Age group	6&7-year-olds	1.3	0.77	1.68	0.092
		8&9-year-olds	2.47	1.28	1.93	0.054
	Actor gender	Male	-1.01	0.76	-1.33	0.183
	Distribution x Age group	Unequal x 6&7-year-olds	-3.58	0.78	-4.61	< 0.001
		Unequal x 8&9-year-olds	-4.25	1.28	-3.33	< 0.001
	Distribution x Actor gender	Unequal x Male	1.62	0.76	2.14	0.032
Advantageous Inequity		Intercept	3.02	0.47	6.47	< 0.001
	Distribution	Unequal	0.59	0.58	1.01	0.311
	Age group	6&7-year-olds	-0.89	0.62	-1.45	0.148
		8&9-year-olds	-0.46	0.63	-0.74	0.460
	Distribution x Age group	Unequal x 6&7-year-olds	-0.51	0.7	-0.73	0.466
		Unequal x 8&9-year-olds	-2.5	0.69	-3.60	< 0.001

Table A3.3. Output from minimal generalized linear mixed model of subjects' decisions in the disadvantageous and advantageous inequity conditions of Study 2. Coefficients indicate the estimated effects of predictors on the response term (accept = 1, reject = 0) relative to the following baseline levels: Distribution = equal; Age group = 4&5-year-old; Order = Equal block first.

Study 2			β	s.e.	z	p
Disadvantageous Inequity		Intercept	2.68	0.29	9.25	<0.001
	Distribution	Unequal	-1.18	0.28	-4.25	<0.001
	Age group	6&7-year-olds	0.07	0.43	0.16	0.876
		8&9-year-olds	-0.01	0.51	-0.03	0.978
	Distribution x Age group	Unequal x 6&7-year-olds	-1.28	0.41	-3.13	0.002
		Unequal x 8&9-year-olds	-0.63	0.48	-1.3	0.193
Advantageous Inequity		Intercept	2.67	0.24	11.15	<0.001
	Order	Unequal block first	-0.88	0.32	-2.78	0.005

Table A3.4 Output from generalized linear mixed model of subjects' decisions in the disadvantageous inequity (DI) and advantageous inequity (AI) conditions. Separate models were run to examine subjects' decisions in a social context (Study 1) compared to a nonsocial context (Study 2). Models examined subjects decisions about equal reward allocations (1-1) or unequal reward allocations (DI: 1-4; AI: 4-1) Coefficients indicate the estimated effects of predictors on the response term (accept = 1, reject = 0) relative to the following baseline levels: Social or nonsocial = nonsocial; Age group = 4&5-year-olds).

			β	s.e.	z	p
DI: Unequal		Intercept	1.63	0.29	5.59	$p < 0.001$
	Social or nonsocial	Social	-1.91	0.50	-3.82	$p < 0.001$
	Age group	6&7-year-olds	-1.37	0.42	-3.28	0.001
		8&9-year-olds	-0.69	0.50	-1.39	0.166
	Social or nonsocial x Age group	Unequal x 6&7-year-olds	4.03	0.72	5.58	0.000
		Unequal x 8&9-year-olds	2.70	0.77	3.51	0.000
DI: Equal		Intercept	3.21	0.40	7.95	$p < 0.001$
	Social or nonsocial	Social	-6.60	0.73	-8.98	$p < 0.001$
	Age group	6&7-year-olds	0.12	0.60	0.20	0.845
		8&9-year-olds	0.13	0.72	0.18	0.859
	Social or nonsocial x Age group	Unequal x 6&7-year-olds	-1.36	1.18	-1.15	0.248
		Unequal x 8&9-year-olds	-2.62	1.84	-1.43	0.154
AI: Unequal		Intercept	2.93	0.55	5.34	$p < 0.001$
	Social or nonsocial	Social	-8.31	1.31	-6.33	$p < 0.001$
	Age group	6&7-year-olds	1.12	0.85	1.32	0.188
		8&9-year-olds	0.92	0.88	1.04	0.298
	Social or nonsocial x Age group	Unequal x 6&7-year-olds	0.31	1.73	0.18	0.855
		Unequal x 8&9-year-olds	3.38	1.63	2.07	0.039
AI: Equal		Intercept	2.26	0.32	6.99	$p < 0.001$
	Social or nonsocial	Social	-5.44	0.61	-8.88	$p < 0.001$
	Age group	6&7-year-olds	-0.05	0.46	-0.10	0.920
		8&9-year-olds	-0.29	0.47	-0.62	0.535
	Social or nonsocial x Age group	Unequal x 6&7-year-olds	0.87	0.84	1.04	0.298
		Unequal x 8&9-year-olds	0.58	0.86	0.68	0.498

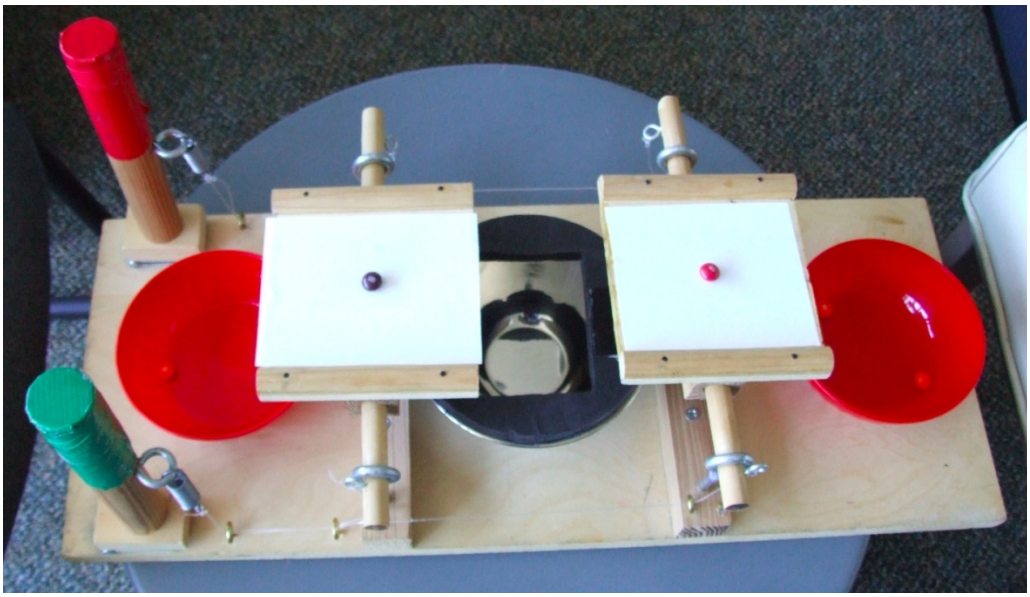

Figure A3.1. Photograph of apparatus used in these studies. Deciders sat on the left side of the apparatus and could operate the handles while the partner (if present) sat on the right side of the apparatus. Pulling the green handle caused the trays to tip outwards, delivering candies to the two outside bowls ("accepting an offer"). Pulling the red hand caused the trays to tip inwards, delivering candy to the inside bowl ("rejecting an offer").

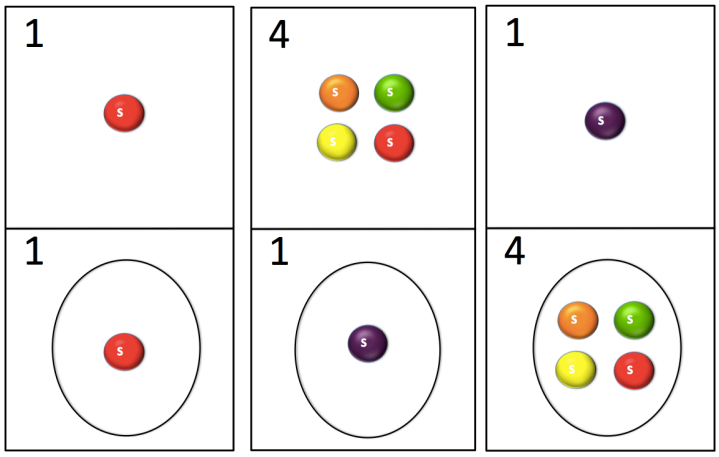

Figure A3.2. Picture of cards used in Study 1 to randomly generate offers. The black circle indicates the decider's reward allocation. From left to right, cards show an equal allocation (1-1), a disadvantageous inequity allocation (DI; 1-4) and an advantageous inequity allocation (AI; 4-1).

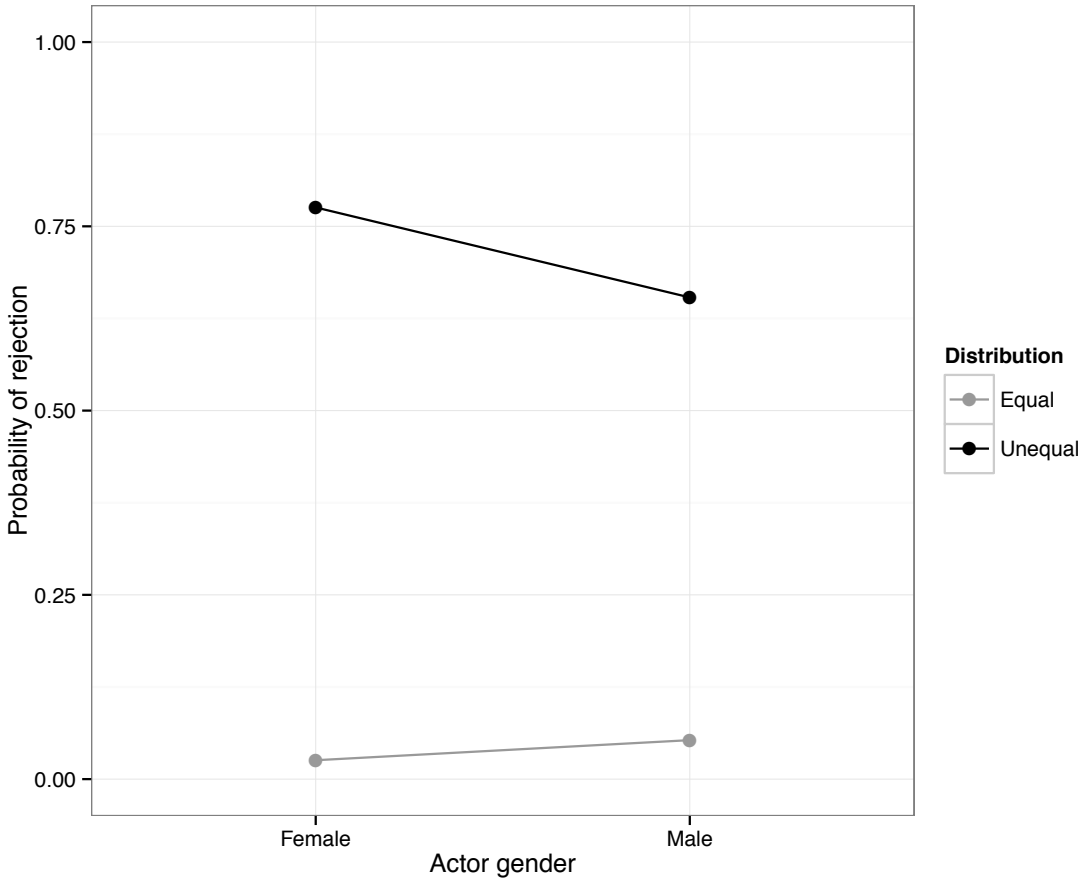

Figure A3.3. Line plots showing the interaction between actor gender and distribution in the disadvantageous inequity condition of Study 1.

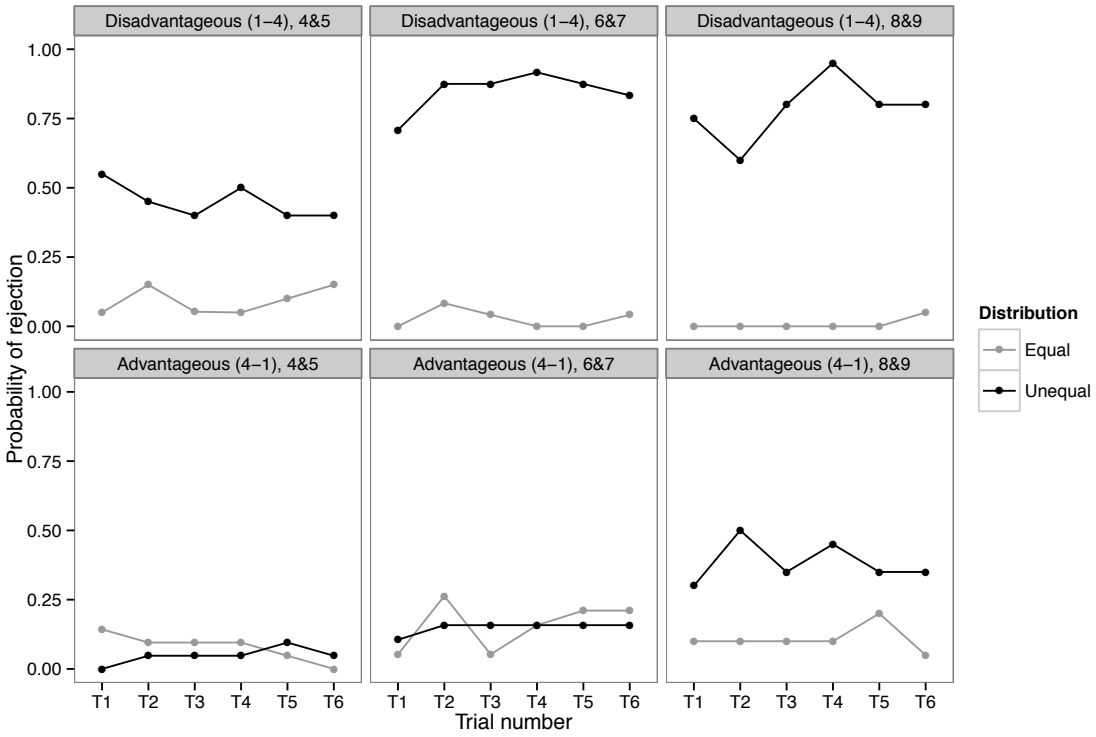

Figure A3.4. Probability of reward allocation rejection over trials in Study 1, in which reward allocations were either generated deliberately by the experimenter or randomly generated by a deck of cards. Rejections are shown across age groups for the disadvantageous inequity (DI) condition (top row) and the advantageous inequity (AI) condition (bottom row). Because offer origin (deliberate vs. random) did not affect subjects' propensities to reject allocations, rejections of deliberate and random allocations are combined here. Subjects were assigned either to the DI condition (N = 64 pairs) or to the AI condition (N = 60 pairs). In the DI condition, subjects received one piece of candy while either one piece (equal distribution) or four pieces (unequal distribution) were placed on the recipient's side of the apparatus. In the AI condition, subjects received either one piece of candy (equal distribution) or four pieces (unequal distribution) while one piece was placed on the recipient's side of the apparatus. In both the DI and AI conditions, subjects received six equal trials and six unequal trials.

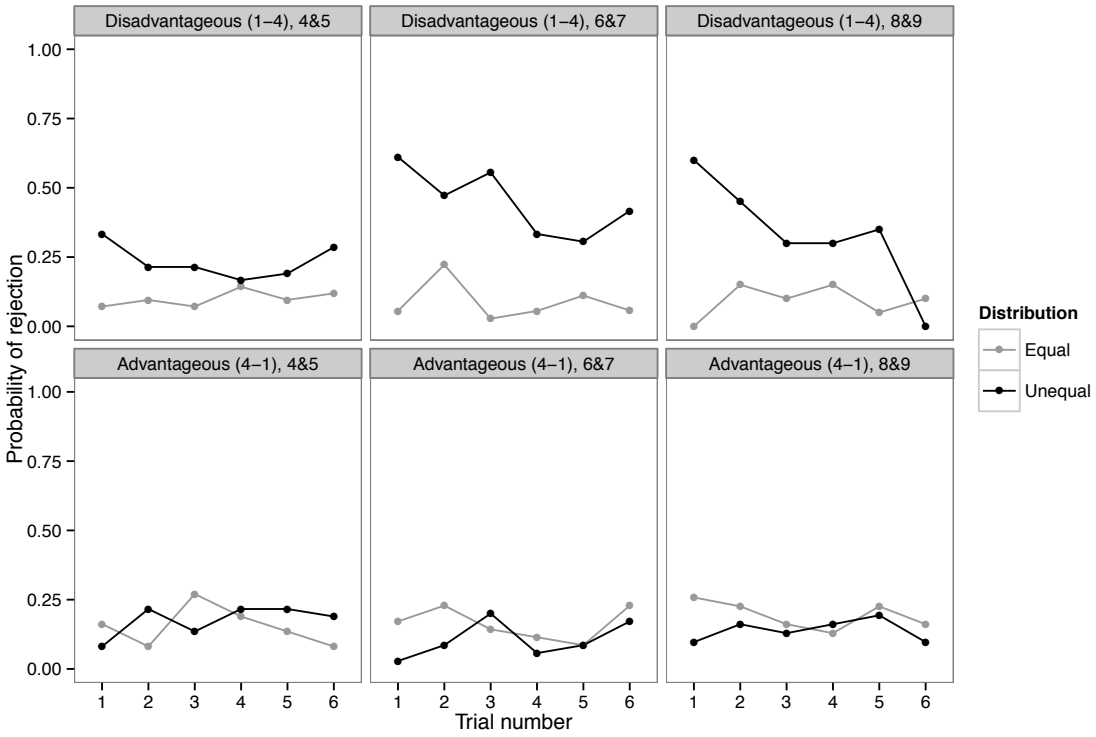

Figure A3.5. Probability of reward allocation rejection over trials in Study 2, the nonsocial version of the inequity game. Rejections are shown across age groups for the disadvantageous inequity (DI) condition (top row) and the advantageous inequity (AI) condition (bottom row). Subjects were assigned either to the DI condition (N = 98) or to the AI condition (N = 103). In the DI condition, subjects received one piece of candy while either one piece (equal distribution) or four pieces (unequal distribution) were placed on the other side of the apparatus. In the AI condition, subjects received either one piece of candy (equal distribution) or four pieces (unequal distribution) while one piece was placed on the other side of the apparatus. In both the DI and AI conditions, subjects received six equal trials and six unequal trials.

APPENDIX 4: SUPPLEMENTARY TABLES AND FIGURES FOR CHAPTER 6

Table A4.1. Sample size by age group, actor gender, recipient gender and condition.

Age Group	Actor Gender	Recipient Gender	Public	Recipient Ignorant	Private	Total pairs
6&7	Female	F	12	9	10	53
		M	8	7	7	
	Male	F	10	10	8	49
		M	7	7	7	
8&9	Female	F	12	11	9	60
		M	8	12	8	
	Male	F	8	7	9	50
		M	7	11	8	
Total pairs			72	74	66	212

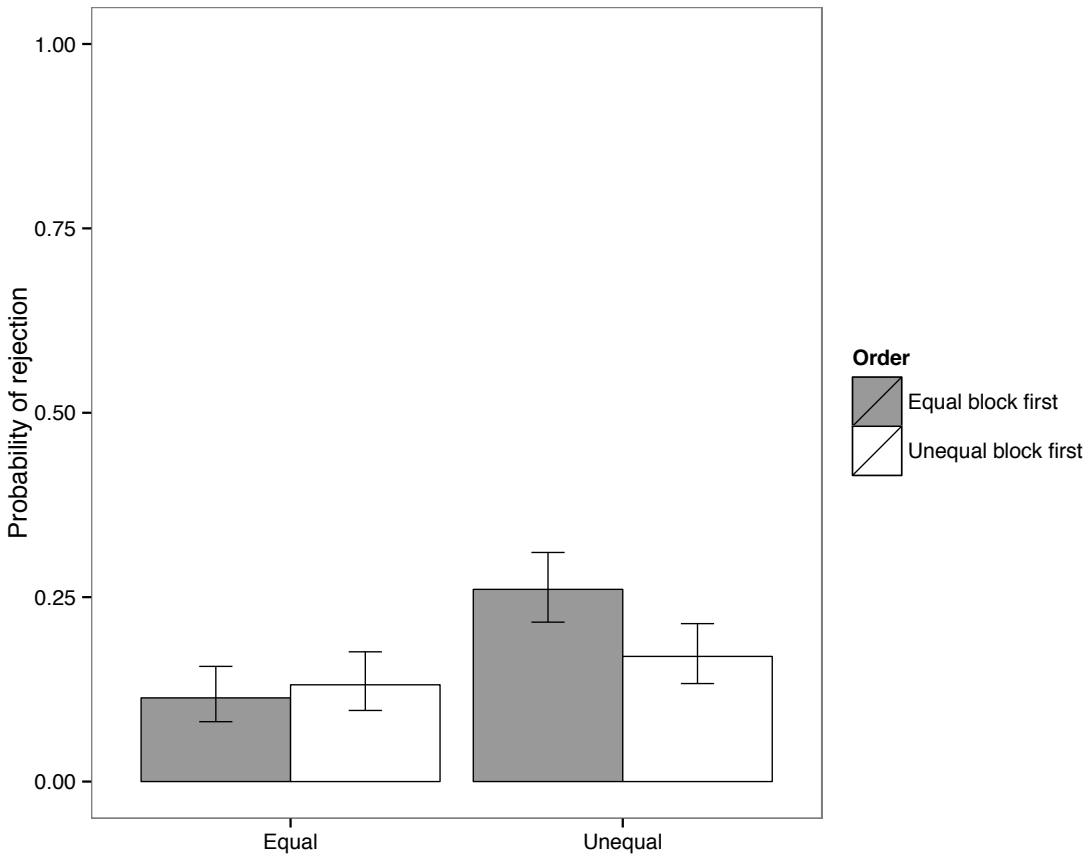

Figure A4.1. Bar plot generated from raw data showing probability of rejections of equal and unequal reward allocations in 6-9-year-old children. Bars show rejections by order in which trial blocks were presented. Children received 6 equal trials (1 candy for decider and 1 candy for recipient) and 6 advantageously unequal trials (4 candies for the decider and 1 candy for the recipient). Trials were presented in blocks and the order in which trial blocks were presented was counterbalanced between subjects. The two possible orders were: block of equal trials first, followed by unequal trials or block of unequal trials first, followed by equal trials. Error bars indicate 95% confidence intervals.